

VOLUME XXXVI

NUMBER 1

JOURNAL  
OF THE  
ARNOLD ARBORETUM  
HARVARD UNIVERSITY

EDITORIAL BOARD

C. E. KOBUSKI, *Editor*

I. W. BAILEY

I. M. JOHNSTON

R. A. HOWARD

KARL SAX

C. E. WOOD

JANUARY, 1955



PUBLISHED BY

THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY  
JAMAICA PLAIN, MASS.

1955



# THE JOURNAL OF THE ARNOLD ARBORETUM

Published quarterly by the Arnold Arboretum of Harvard University.

Subscription price \$7.00 per year.

Vols. I-XI out of print. Vols. XII (1931), XIII (1932): Price \$3.00 each. Vols. XIV (1933) — XXVIII (1947): Price \$4.00 each. Vols. XXIX (1948) — XXXV (1954): Price \$7.00 each.

Subscriptions and remittances should be addressed to the ARNOLD ARBORETUM, JAMAICA PLAIN, MASSACHUSETTS.

---

## CONTENTS OF NO. 1

A FOURTH TYPE OF NODAL ANATOMY IN DICOTYLEDONS, ILLUSTRATED BY CLERODENDRON TRICHOTOMUM THUNB. With one plate. By <i>Margery P. F. Marsden and I. W. Bailey</i> .....	1
A MONOGRAPH OF THE GENUS PHILADELPHUS (Continued). By <i>Shiu-ying Hu</i> .....	52
INDUCTION OF EARLY FLOWERING OF ORNAMENTAL APPLE TREES. By <i>Karl Sax and Albert G. Johnson</i> .....	110
RHODODENDRON MACROPHYLLUM D. DON EX G. DON. By <i>Leonard F. Frisbie</i> .....	115

---

Vol. XXXV, No. 4, including pages 275-390, with four plates, Title-page, and Table of Contents, was issued October 15, 1954.

---

Entered as second class matter April 4, 1940, at the post office at Boston, Massachusetts, under the Act of August 24, 1912.

---

# JOURNAL

## OF THE

# ARNOLD ARBORETUM

---

VOL. XXXVI

JANUARY 1955

NUMBER 1

---

### A FOURTH TYPE OF NODAL ANATOMY IN DICOTYLEDONS, ILLUSTRATED BY CLERODENDRON TRICHOTOMUM THUNB.

MARGERY P. F. MARSDEN \* AND I. W. BAILEY

*With one plate and seventeen figures*

#### INTRODUCTION

IN 1914, Sinnott demonstrated by an analysis of 34 orders and 164 families that there are three significant forms of foliar nodal anatomy in dicotyledons, viz. (1) the *unilacunar* form in which the vascular supply of the leaf is related to a single gap in the stele, (2) the *trilacunar* form in which the vascular strands are related to three distinct and more or less widely separated gaps, and (3) the *multilacunar* form in which five or more vascular strands are related to as many independent gaps. Although various dicotyledonous families are prevaillingly unilacunar, trilacunar or multilacunar — thus providing significant evidence in the identification and classification of plants — there is a considerable number of families and many orders in which transitions between the different forms of nodal anatomy occur. Sinnott concluded that the trilacunar condition is primitive in angiosperms, the multilacunar form (much modified in monocotyledons) having arisen by amplification of the number of independently attached lateral strands, and the unilacunar form (a) in certain families by reduction and elimination of the two lateral strands and (b) in other families by the approximation of the median and lateral strands forming an aggregation of three strands that is related to a single gap in the stele.

Using this conclusion as a basis, Sinnott and Bailey (1914, 1915) attempted to demonstrate by statistical correlations that the primitive angiospermic leaf was simple and palmately veined. Subsequently, Eames (1931) adopted the concept of a primitive trilacunar condition as a working hypothesis in the study of floral morphology. Thus, nodal anatomy became part of the foundation for considerable phylogenetic investigation.

Recently, studies of the Austrobaileyaceae (Bailey and Swamy, 1949),

\* This investigation was supported in part by a fellowship from the English-Speaking Union, and by the Fanny Bullock Workman Fellowship from Radcliffe College. Part of this paper represents a portion of a thesis submitted for the Ph.D. degree in Radcliffe College to the Department of Biology, Harvard University.



Monimiaceae (Money, Bailey and Swamy, 1950) and Chloranthaceae (Swamy and Bailey, 1950; Swamy, 1953a) have revealed patterns of foliar vasculature which necessitate a comprehensive reassessment of the significance of nodal anatomy in the phylogeny of the angiosperms.

The leaves of the majority of dicotyledons, as indicated by Sinnott, are vascularized by what appears at the nodal level to be an odd number (1, 3, 5, 7, etc.) of discrete vascular strands. On the contrary, the leaves of *Austrobaileya*, *Trimenia*, and *Ascarina* are vascularized by two independent strands that are related to a single gap at the nodal level. Since similar structures occur in various gymnosperms and in the cotyledonary node of many dicotyledons, it is essential to determine whether the foliar unilacunar nodes of dicotyledons have been derived in all cases from a trilacunar one.

Most of the work in the past has dealt with comparative investigations of fully matured structures at nodal levels. Such comparative studies of end-products without comprehensive developmental investigations at successive levels of the shoot and leaf, may be misleading. What is needed in the study of the evolution of various plant organs, as well as of the plants as a whole, is "a phylogeny of successively modified ontogenies." Therefore it is essential to obtain an accurate developmental picture of plants which have a double leaf trace at their unilacunar nodes. Being unable to obtain viable seeds of such ranalian genera as *Austrobaileya*, *Trimenia* and *Ascarina*, it seemed desirable to make a comprehensive study of the vascularization of *Clerodendron trichotomum* Thunb. of the Verbenaceae, which has at maturity a similar type of nodal anatomy.

#### MATERIAL AND METHODS

**Adult plant:** Abundant material was obtained from shrubs of *Clerodendron trichotomum* Thunb. in the Rare Plants section of the Arnold Arboretum. Weekly collections of buds, nodal material, and young and mature leaves were made from March 20 to about September 15, 1952, and after this, collections of buds were made irregularly until March, 1953.

The morphology of *C. trichotomum* has been described by Lam (1919). The material used for our studies, however, does not completely agree with his description, since the three-lobed leaves which he records have never been observed in adult specimens, but large-lobed juvenile leaves have been observed on two-year-old plants grown from seed. Specimens of the plants used in these investigations have been placed in the herbarium of the Arnold Arboretum.

The plants of *C. trichotomum* are shrubs 8 to 10 ft. in height, which branch profusely, particularly from the base of the main stem. The leaves are arranged in an opposite and decussate manner; they are simple, lanceolate to ovate, slightly serrate and have reticulate venation. The lamina of adult leaves is approximately 8 cm. long, while that of the juvenile ones is approximately 12 cm. long. The petioles are frequently as long as the leaves.



In the axil of each leaf there is a lateral bud complex. This consists of one main bud with one pair of subsidiary buds, lateral to it, and usually one additional sub-lateral bud. From these aggregations of buds lateral branching often occurs near the base of the shoot, in one- and two-year-old plants.

The inflorescence is a many-flowered cymous panicle, and is trichotomous. Each of the lateral cymes arises in the axil of a foliage leaf. Reduced scale-like bracts subtend the higher divisions of the inflorescence; these are caducous.

**Seedling:** Originally, supposedly fresh seed of *C. trichotomum* was obtained through a commercial seed house. Some of this seed was planted in seed pans in the greenhouses of the Biological Laboratories, Harvard University. Other samples of the same seed were presoaked, scarified, or given cold treatment at 5 degrees C. in moist peat for 6–8 weeks to allow after ripening. In all cases germination occurred in less than 3% of the seeds planted.

The next fall ripe fruits were collected directly from the shrubs in the Arnold Arboretum. The seeds were removed, immediately planted on the surface of soil, and covered by damp sphagnum moss. They were planted in mid-October and were kept in the greenhouses of the Arboretum. By mid-December approximately 10% of the seeds planted had germinated. Germination continued until by mid-January approximately 70% of the seeds had germinated.

There appears to be no description of the fruit, seed, or seedling of *C. trichotomum* in the literature, although the seed and seedling of *C. Kaempferi*, Fisch. has been described by Lubbock (1892). This description differs so markedly from *C. trichotomum* (probably because Lubbock failed to recognize that *C. Kaempferi* is hypogeal in germination) that the following description of *C. trichotomum* is given here.

The fruit is formed from a gynoeceum which consists typically of four carpels. There is a single loculus and each carpel usually bears two ovules; however, in the fruit there are never more than four seeds and frequently only two or three. Each seed has an extremely hard and sclerotic testa which is sculptured on one side, and smooth with a deep longitudinal groove on the other side. Through this groove the fleshy funicle attaches the seed to the placenta. On germination the radicle emerges through this longitudinal groove, which also marks the line of weakness along which the testa eventually splits. The seed is non-endospermic and the cotyledons are large and fleshy.

Germination is hypogeal (see PLATE I:3). Shortly after the radicle emerges through the longitudinal slit, the shoot appears above the surface of the ground with its tip bent over (PLATE I:3c, d). The epicotyl straightens, elongates and carries the first pair of leaves upwards (PLATE I:e, f). The fleshy cotyledons remain underground enclosed in the testa; after about three months they shrivel and become detached.

The hypocotyl is minute, 2–3 mm. long, 2 mm. thick, and glabrous. The epicotyl (i.e., between the point of attachment of the cotyledons and the

first pair of leaves) is 4.5–6 cm. long, pale green and pubescent. The cotyledons are stalked (petiole 3–5 mm. long, lamina 8–10 mm. long), white, fleshy, ovate, entire, without obvious venation; they are enclosed in the testa. The root is a tap root bearing many lateral branches. The first internode of the stem is 4.25–6 cm. long, the second 2–3 cm. long and subsequent internodes are 1 cm. long or less. The stem is cylindrical, bright green, pubescent. The leaves are simple, opposite and decussate, exstipulate and petiolate. The petiole is very long; the lamina and petiole are pubescent on both surfaces. Leaves at the first node are suborbicular, pale green, larger than the cotyledons with margins irregularly toothed towards the apex. At the second node leaves are rhomboidal to ovate and the margins are irregularly toothed. The third pair of leaves resembles the adult leaves which are ovate and irregularly toothed.

**Histological techniques:** Seedling, foliar and nodal material was fixed in formal acetic alcohol, medium chromo-acetic and strong chromo-acetic alcohol (Johansen, 1940). A modified Zirkle's n-butyl alcohol method for dehydrating refractory plant material was employed and subsequently the paraffin-tissue-embedment method described by Pratt and Wetmore (1951) was used for embedding the material. Hard tissues were presoaked in water before sectioning. Embedded material was sectioned on a Spencer rotary microtome at 8 to 10 micra. Egg albumen fixative was used for mounting the serial sections, and preparatory to staining the slides were coated with a 1/2% solution of paraloid in ether.

Staining combinations used for serial sections were as follows: — Heidenhain's iron-alum haematoxylin with safranin as a counterstain (Jeffrey, 1917); 1% safranin counterstained with picro-aniline blue (1 gm. water soluble aniline blue to 100 cc. of 80% ethyl alcohol with 1 cc. of saturated aqueous picric acid); 1% safranin and a saturated solution of cotton blue in lactophenol. In very young material where it was desired to emphasize meristematic tissues, as for example in seed and seedling sections, Foster's (1934) tannic acid and ferric chloride technique was employed.

Foliar material was cleared by use of a 5–8% NaOH solution (Bailey and Nast, 1943). In the case of seedling material, clearing methods involving the use of lactic acid (Debenham, 1939) have been found to be more satisfactory than the NaOH method. A basic fuchsin stain was used in some cases to accentuate the vascular pattern (De Tomasi, 1936; Kumar et al., 1942).

#### VASCULARIZATION OF SEED AND SEEDLING

**Seed:** Seed obtained directly from shrubs in October was examined by means of serial sections since the fleshy cotyledons are difficult to clear without damage to the delicate epicotyl and radicle. At the cotyledonary node each cotyledon possesses two distinct procambial<sup>1</sup> strands (FIG. 1:A). Four vascular strands differentiate behind the shoot apical meristem as it

<sup>1</sup> The criteria used by Esau (1942, 1943a, and 1943b) for the identification of the procambium, first-formed xylem, and first-formed phloem have been followed in this investigation.



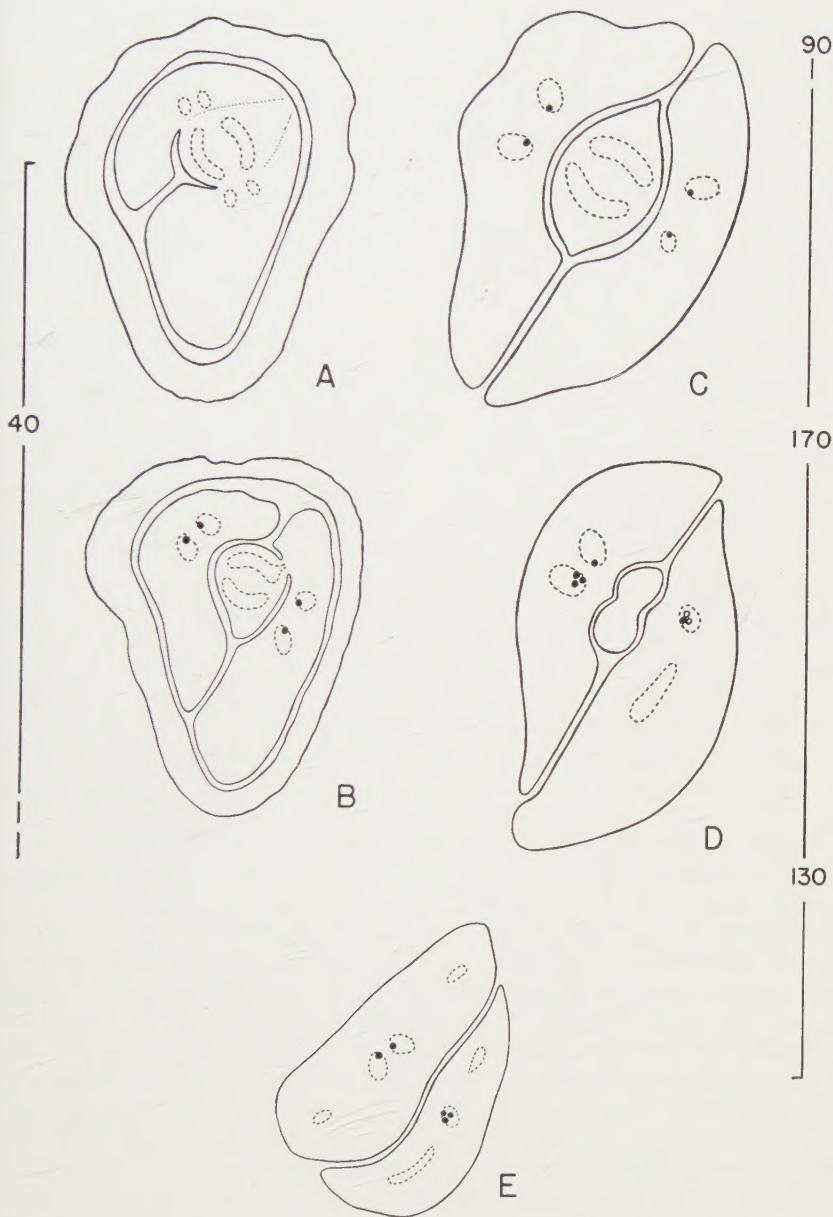


FIGURE 1

SERIES OF SECTIONS OF THE SEED OF *Clerodendron trichotomum*. Procambium is represented within the dotted lines, and first xylem elements as black dots. The distance in micra between sections is shown on the left and right.

elongates but at this early stage these are not obvious and the procambium has the appearance of an indistinct cylinder. The procambium of the root forms a solid central core.

At the cotyledonary node the procambial cylinder forms two arcs (FIG. 1:A); the gaps in the procambial cylinder occur at the points of attachment of the two cotyledons. At this stage there is no differentiation of xylem in the epicotyl, in the cotyledonary node nor in the bases of the cotyledons. In the radicle, which is much larger and better developed than the shoot, four spiral or annular xylem elements differentiate about 800 micra below the cotyledonary node in the position of the protoxylem points of a tetrach root.

Approximately 50 micra above the cotyledonary node two protoxylem elements differentiate in each cotyledon, one in each of the procambial groups (FIG. 1:B). At a distance of 100 micra above the cotyledonary node additional elements appear in the procambial strands of the cotyledons, and between 100 and 250 micra each may possess as many as three parallel xylem elements (FIG. 1:D). At this level, and above, lateral procambial strands depart so that the entire vascular pattern of each cotyledon is laid out (FIG. 1:E). Between 250 and 300 micra, however, differentiation is less, until finally at 350 micra no protoxylem elements can be observed, although the procambial strands remain distinct.

**First seedling stage:** Approximately two months after the seeds have been planted the radicle emerges from the longitudinal slit in the testa. Seedlings which are examined at this stage when the radicle is only a few millimeters long (PLATE I:3b) show that the differentiating xylem in the cotyledons links with that in the root. The shoot, which has grown very little, still possesses a distinct procambial pattern but shows no differentiation of first-formed xylem. Two distinct xylem groups are present in each cotyledon well above the cotyledonary node and these differentiate acropetally towards the tip of the cotyledon and basipetally towards the cotyledonary node. The two procambial strands in each cotyledon may remain distinct for its entire length, or, as is more usual, they coalesce towards the tip of the cotyledon. Similarly the differentiating xylem remains distinct for some considerable distance, but towards the tip there is usually a single spiral first-formed xylem element. At about 400 micra from the cotyledonary node the maximum number of xylem elements is observed, and here there are two distinct first-formed xylem elements which are usually spiral in thickening and which are located towards the inside of each of the procambial groups. Two or three late-formed primary xylem elements may also differentiate at this level in the cotyledons and development is centrifugal towards the margin of the cotyledon.

Later differentiation between the region of initial maturation in the cotyledons and the cotyledonary node is basipetal. Frequently the newly formed xylem nearer the cotyledonary node is scalariform and therefore probably "late formed primary xylem."<sup>2</sup> Spiral and annular xylem ele-

<sup>2</sup> It is well known that the term protoxylem is used to denote the first-formed xylem in plants, and that although this frequently exhibits spiral and annular thicken-



ments always drop out of the cotyledonary traces as they are followed downwards through the node.

The *transition region* of a very young seedling before epicotyl elongation exhibits much the same form as that in an older seedling where the shoot becomes vascularized. The procambium in the epicotyl is divided into four distinct strands (FIG. 2:1). At the cotyledonary node each trace from the cotyledons passes in towards a separate procambial strand from the epicotyl (FIG. 2:2) and joins with it (FIG. 2:2). Below the cotyledonary node the four partially differentiated vascular bundles remain distinct; if any protoxylem is present the arrangement is endarch. Between 300 and 700 micra below the cotyledonary node any spiral or annular xylem related to the cotyledonary traces drops out, and four distinct annular xylem elements appear in the position of the protoxylem poles of the root, i.e., in the gaps between the vascular bundles of the hypocotyl (FIG. 2:4, 5, 6). These protoxylem traces are in no way connected with the cotyledonary traces but extend upwards from the protoxylem points of the root protostele. They usually extend farther up in the gaps at right angles to the median axis of the cotyledons than in the gaps between the two traces of each cotyledon (FIG. 2:5).

At the cotyledonary node the phloem lies on the same radius as the meta- and protoxylem and remains in the same position throughout the hypocotyl and into the root. In the hypocotyl the internal annular elements along this radius drop out, leaving collateral bundles of phloem and scalariform xylem (FIG. 2:4-7). Passing downwards these bundles approach each other about the center of the axis until a solid xylem core is formed surrounded by the same four strands of phloem (FIG. 2:7, 8). Meanwhile new protoxylem strands have appeared along radii alternate with the collateral bundles (FIG. 3); these become the protoxylem poles of the tetrach root (FIG. 2:8). Hence the first-formed xylem of the shoot is not continuous with that of the root, but joins with metaxylem from the root at a level in the hypocotyl at which protoxylem strands from the root protoxylem poles have already been differentiated. This fact is illustrated in figures 2 and 3.

It is quite obvious that the transformation of vascular pattern from the true root to true stem condition described for *Clerodendron trichotomum* in no way corresponds to the "transition types" postulated by Van Tieghem (1891); nor has any twisting, rotation or inversion been observed such as is described by Eames and MacDaniels (1947), Lenoir (1920), or Van Tieghem (1891). These workers regard the vascular system of the seedling plant as a single unit which is morphologically equivalent in all its parts. The observations in this study seem rather to uphold the work of Dangeard (1889, 1913) in which he indicates that the seedling system is initially discontinuous. He considers that this system consists of a ra-

ings, this is not necessarily always the case. However, spiral and annular elements usually differentiate in tissues which are undergoing elongation, and scalariform and pitted elements in tissues which have ceased such growth (as recently indicated by the work of Smith and Kersten, 1942).

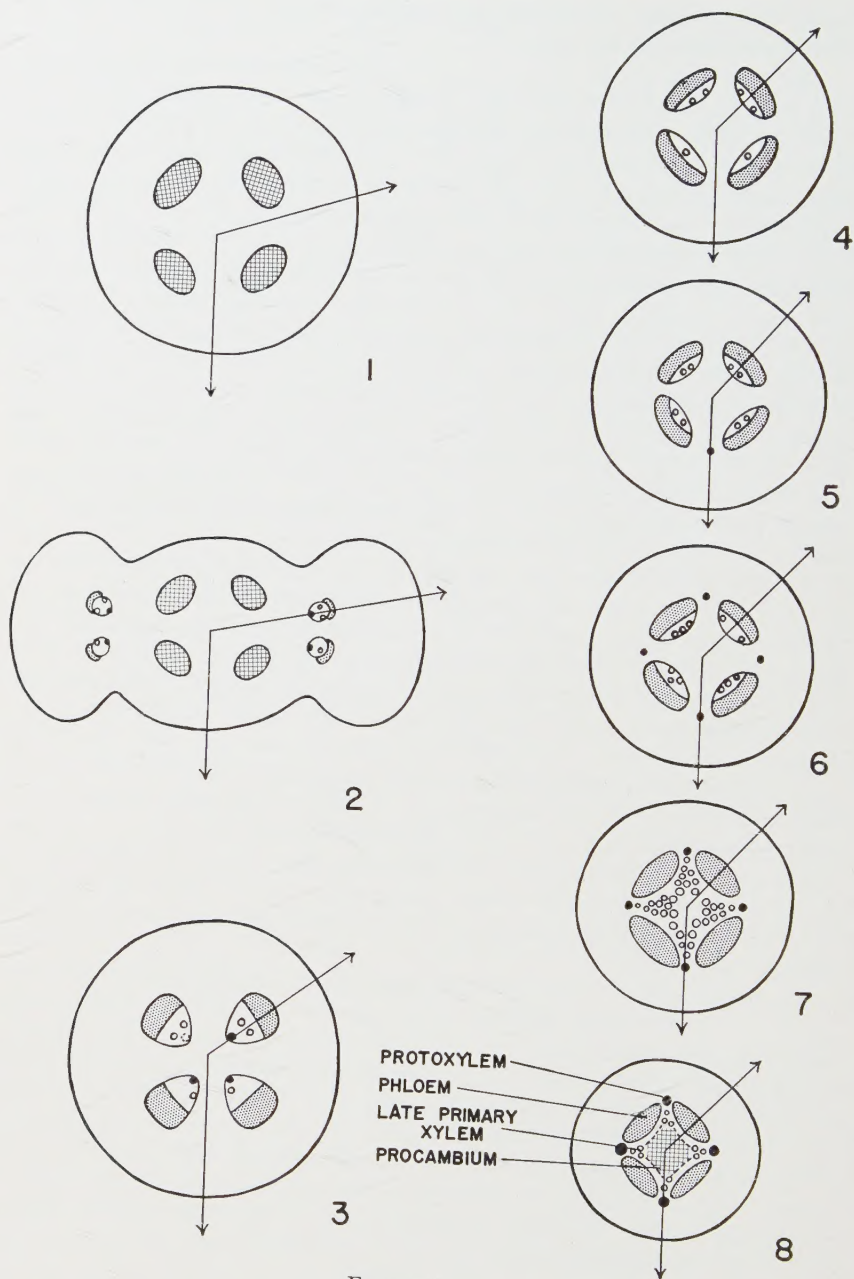


FIGURE 2

SERIES OF SECTIONS THROUGH THE TRANSITION REGION OF A SEEDLING OF *Clerodendron trichotomum*. The arrows indicate the direction of the diagram in figure 3.



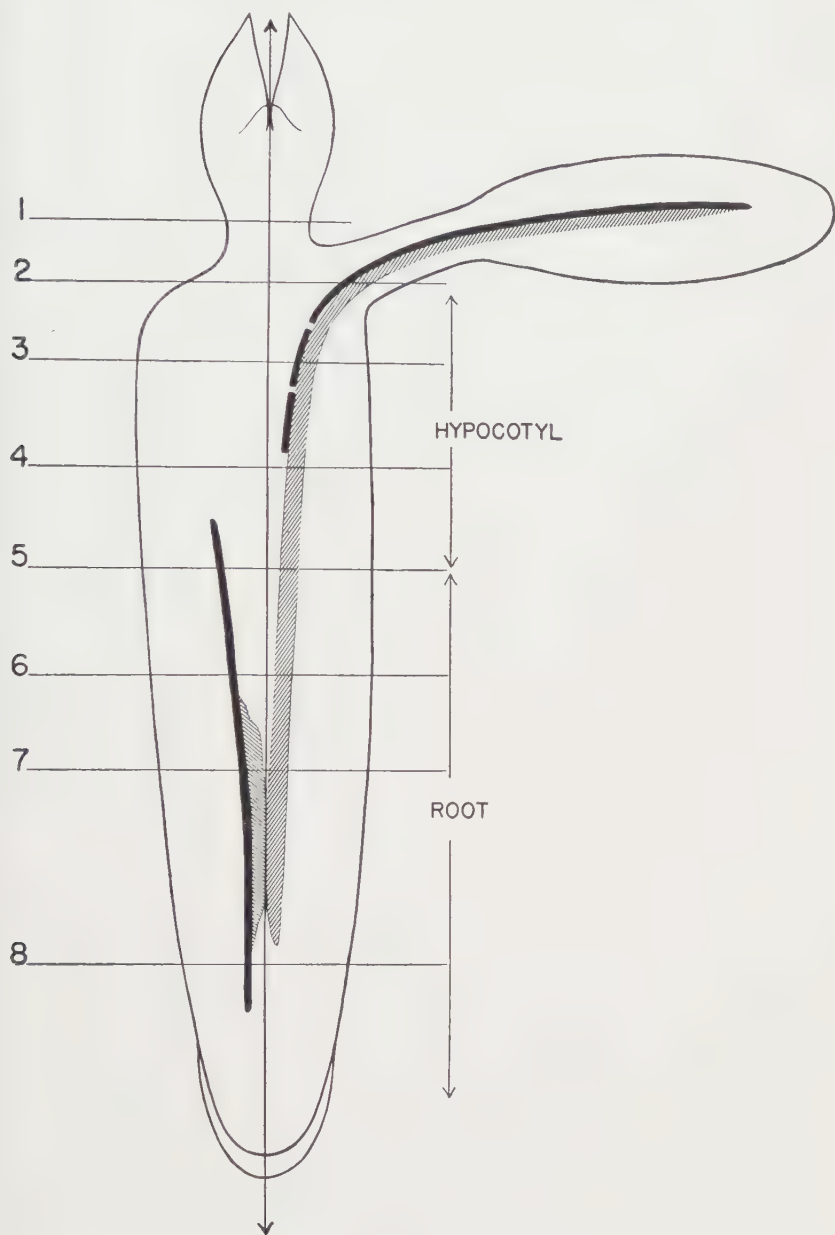


FIGURE 3

LONGITUDINAL SECTION OF THE SEEDLING OF *C. trichotomum* (DIAGRAMMATIC) SHOWING THE POSITION OF THE SECTIONS IN FIGURE 2. First xylem elements are shown in black, later formed xylem is striped. The direction of the diagram is shown on the transverse sections in figure 2.

dicular hypocotylary part and a cotyledonary part and that these two are joined in the upper hypocotyl. This condition would appear to be comparable with the vascular ontogeny observed in *C. trichotomum*. Chauveaud (1911, 1921) also records discontinuity of protoxylem in the majority of the seedlings which he investigated. Paxson (unpublished) found discontinuity of protoxylem in seedlings of *Cucurbita texana*. Lehmberg (1923-24) observed no twisting or rotation of xylem and phloem groups in the transition region of seedlings of *Helianthus annuus*, although the arrangement and number of traces in *Helianthus* does not correspond with those observed in this investigation on *Clerodendron* seedlings.

The arrangement observed by Hill and de Fraine (1913) and Thomas (1907, 1914), where a median protoxylem cotyledonary pole forms the protoxylem point in the root, is not comparable with the condition previously described for *C. trichotomum*. At the stage of development of the seedling where the epicotyl has not elongated, there is no differentiation of protoxylem in the shoot but the xylem of the cotyledons and root are more or less continuous. Compton (1912) and Muller (1937) examined certain hypogeal leguminous seedlings and observed that the transitional characteristics of the vascular system extended quite far up into the epicotyl, sometimes through more than one internode. In *C. trichotomum*, however, vascularization of the transition region is completed before the epicotyl elongates, and although this plant also is hypogeal, the transition region does not extend above the cotyledonary node.

Thoday's (1939) physiological theory explained the separate centers of differentiation in a seedling. He suggested that the two opposite poles of the axis, viz. of the root and of the shoot, are capable of impressing their own pattern on the meristematic tissues which they produce, and that the leaf primordia and cotyledons influence the structure of the upper part of the seedling axis, as does the root at the base. In *C. trichotomum* where the epicotyl elongates only after the cotyledons, transition region and root are vascularized, it would appear that the pattern is determined principally by (independent) influences arising in the cotyledons and the root.

In only one of about 30 seedlings studied was there any indication of a median annular or spiral xylem element between the double procambial groups of the cotyledons. In this seedling the median protoxylem element was separated from the endarch cotyledonary protoxylem by parenchyma and was not associated even at a later stage with any metaxylem or phloem. The median protoxylem was also stronger below the cotyledonary node, and was connected with the protoxylem strands which alternate with the collateral bundles in the hypocotyl and extend down to form the protoxylem poles of the root. It would therefore seem best to interpret this median "trace" as an upward extension of the protoxylem of the root which ordinarily terminates in the hypocotyl, and not as a true cotyledonary trace. It is possible that such a condition would arise when the root elongates slowly permitting the center of differentiation in the root to impress its pattern at a higher level in the hypocotyl than is ordinarily the case (see Thoday, 1939).



**Vascularization of the seedling shoot:** Serial sections and cleared specimens of seedlings which possess only one pair of leaf primordia exhibit two distinct procambial strands in each of the young leaves. In the epicotyl the procambium differentiates in four distinct bundles and shortly after these are formed the first phloem starts to differentiate. At the base of each of the leaf primordia a spiral or annular xylem element differentiates in each of the two procambial groups, although this may not occur simultaneously in the four procambial strands. Differentiation of these first-formed xylem elements then proceeds towards the leaf tip, and simultaneously, down the epicotyl towards the cotyledonary node.

By following serial transverse sections through the first pair of leaves and shoot apex, one observes that additional elements, spiral, annular and pitted, may extend approximately 600 micra above the level of the apical meristem (FIG. 4:A). At the base of each leaf primordium there are always two separate groups of elements (FIG. 4:C, D), even though the two may fuse and or branch higher in the leaf. Above the point of departure of the leaf traces there are only two arcs of procambial tissue in the stem apex (FIG. 4:D). The gaps lie opposite the leaf primordia and each pair of leaf traces passes in through one gap in the stem procambium (FIG. 4:D). The two traces from each leaf join the procambial arcs of the stem, and then approach each other and become connected tangentially by procambium; so that a cylinder of procambium with four endarch strands of protoxylem is formed (FIG. 4:E). Below the node this opens to give four separate procambial strands (FIG. 4:F), down which the protoxylem is progressively differentiating towards the cotyledonary node. It should be pointed out here that the procambial pattern of the shoot appears to be laid down by continuous acropetal differentiation of epicotylary procambial bundles close behind the apical meristem. This is to be contrasted with the strongly discontinuous differentiation of the first-formed xylem described above.

Each procambial group in the epicotyl shows the differentiation of only one or two xylem elements. In cleared specimens it appears that the spiral and annular xylem in most cases is discontinuous, and in this very early stage the pitted xylem can also be discontinuous. As differentiation proceeds the vascular strands become continuous from the leaves through the epicotyl to the cotyledonary node. In all seedlings examined each foliar strand connects with a separate procambial strand of the epicotyl and becomes a separate vascular bundle.

**The cotyledonary node in the young condition:** In seedlings of the age just described, the differentiation of spiral and annular xylem between the epicotyl and cotyledonary node is not complete and continuous. It is not until the second pair of leaves become vascularized that the xylem of the epicotyl becomes connected with that in the cotyledonary node. No spiral or annular elements differentiate in this region probably since elongation of tissues in the cotyledonary near nodal region is complete, so that only xylem of the pitted type is formed. Moreover, the first scalariform

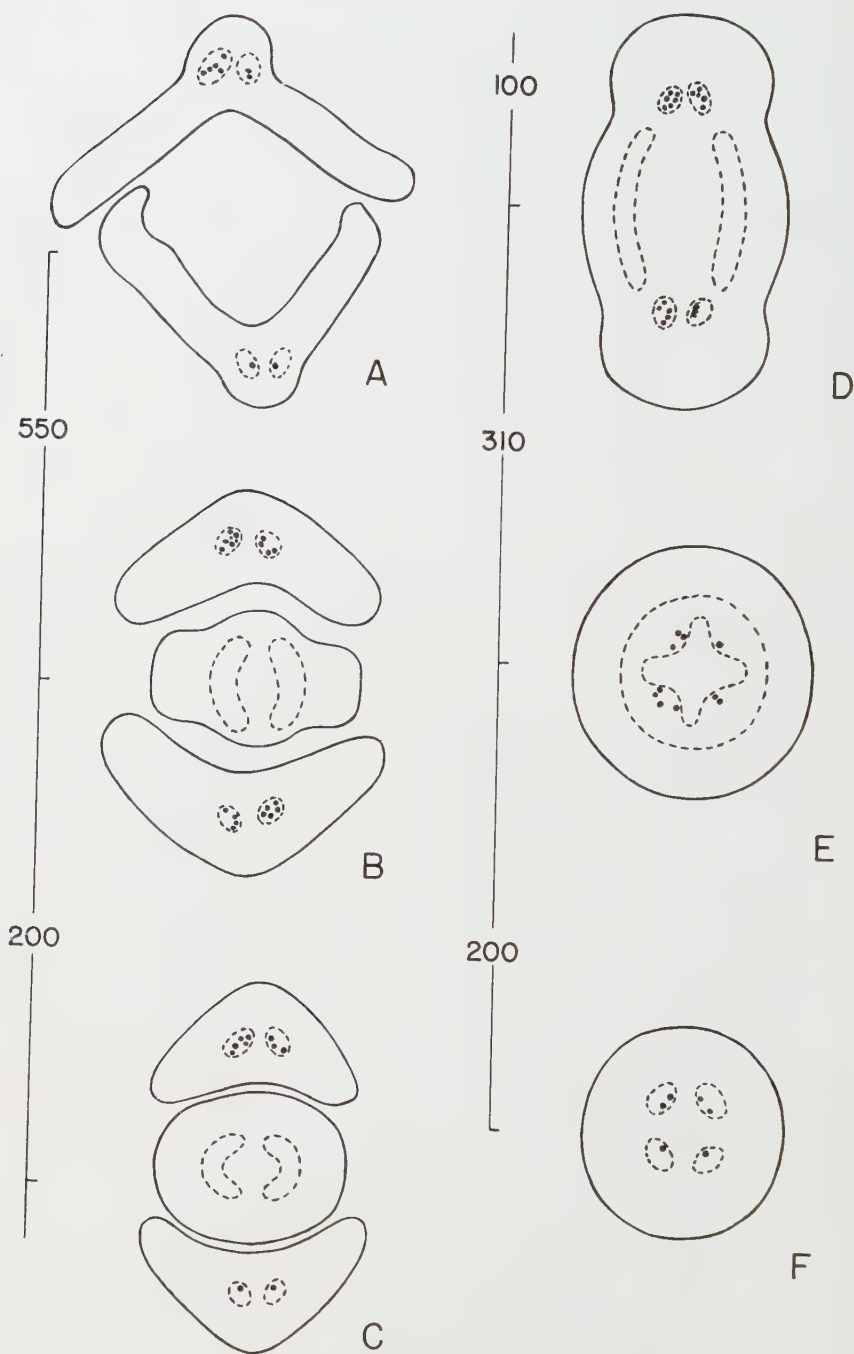


FIGURE 4

A SERIES OF SECTIONS THROUGH THE EPICOTYL OF A YOUNG SEEDLING OF *Clerodendron trichotomum*. Procambium is shown within the dotted lines. First formed xylem elements are represented as black dots. The distance in micra between sections is shown on the left.



xylem to differentiate at the base of the epicotyl becomes continuous with the late-formed primary xylem in the upper portion of the hypocotyl.

**Leaf vascularization in older seedlings:** In seedlings possessing two pairs of leaves on an epicotyl from 4.5–6 cm. long, the complete vascular connection between the epicotyl and root has occurred. As in the first pair of seedling leaves, the leaves of the second pair each possess two procambial strands. Near the level of the apical mound differentiation of vascular tissue occurs in the second leaf pair in a manner identical with that in the first pair of leaves. A few hundred micra above their bases, these leaves possess several spiral, annular and scalariform elements which may or may not be arranged in two distinct groups. But approximately 200 micra above the leaf base and from here downwards, the differentiating xylem groups are quite distinct. About 200 micra below the apical meristem the leaves attach to the stem and the two strands of each leaf, with 1–4 differentiated xylem elements, join with shoot tip procambium through one gap opposite the leaf base. A small bud procambial trace appears in the axil of each leaf primordium (FIG. 5:D).

At about 120 to 150 micra below the origin of the youngest leaf primordia the leaf trace procambium merges with the epicotyl procambium (FIG. 5:E, F) to form (approximately 100 micra below) a complete cylinder (FIG. 5:G). The protoxylem traces of the youngest pair of leaves now form the protoxylem points of the tip of the epicotyl, and each trace from each bundle of the leaf again forms a separate conducting system which never fuses nor runs together with the other strands for their entire course through the shoot.

Approximately 600 micra below this, the procambial cylinder opens and two procambial bud traces pass out to minute buds in the axil of the first pair of seedling leaves (i.e. the oldest pair of leaves). The shoot at this level now possesses two procambial arcs, each with two xylem groups (consisting of 3 or 4 elements from the youngest pair of leaves) which are continuing to develop acropetally towards the region of maximal area of the second node. 150 to 200 micra below this, the region of maximal area (of the first-formed node) is encountered and at this level two xylem traces of 5–8 elements enter the stele from each leaf base through a unilacunar gap. Now eight distinct xylem groups appear in the procambial cylinder of the shoot and these remain very obvious for about 600 to 800 micra below the region of maximal area of the first node. In cleared specimens the four traces from the youngest pair (second pair) of leaves do not appear to extend much below this point.

**Secondary condition superimposed:** The picture becomes extremely difficult to interpret in subsequent stages since seedlings possessing more than two pairs of leaves show initiation of cambial activity. Seedlings with only two pairs of leaves have been examined in which cambial activity has already occurred.

The eight xylem groups appearing in the procambial cylinder as described above eventually link with each other at the base of the epicotyl to form four strands just above the cotyledonary node. They do, how-

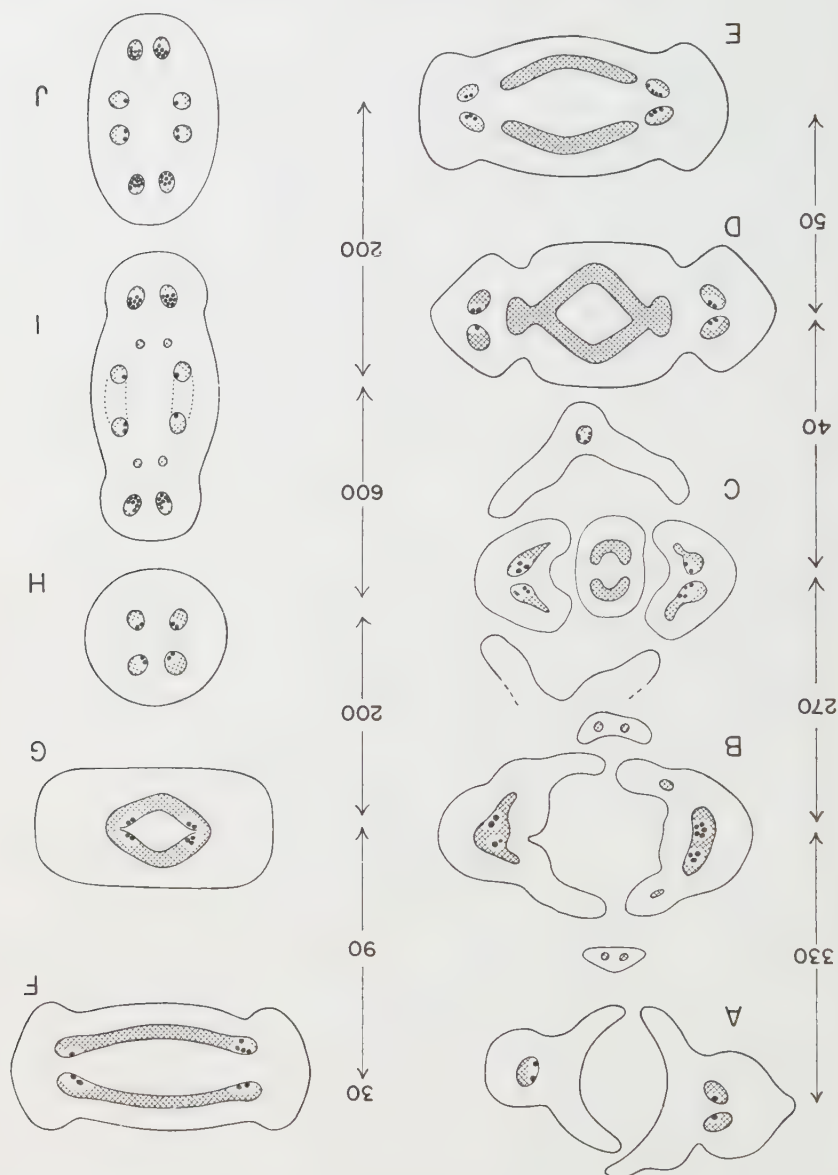


FIGURE 5

SERIES OF SECTIONS THROUGH THE SEEDLING SHOOT TIP WITH TWO PAIRS OF LEAF PRIMORDIA. (*C. trichotomum*). The procambium is shown cross-hatched. First xylem elements are represented in black. The distance in micra between sections is shown on the left.



ever, become connected as a result of secondary activity at a higher level in the epicotyl when a xylem cylinder is formed.

**Vascular connection at the cotyledonary node:** Careful study of cleared seedlings has shown that the acropetally differentiating pitted elements at the base of the epicotyl become continuous with the cotyledonary traces just below the point of attachment of the cotyledons. The differentiation of spiral and annular elements ceases about 1000 to 1500 micra above this region. However, the pitted elements continue in their acropetal differentiation and two or three parallel elements are apparent in each of the four stem strands. Towards the cotyledonary node the number of pitted elements is reduced so that only one or two elements of each strand become continuous with the pitted elements of the cotyledonary traces. The epicotylary traces join the cotyledonary traces on the inside. In many cases this junction with the cotyledonary traces may be coincident with the differentiation of further strands of pitted xylem centripetally in the lower hypocotyl to form the typical exarch root which possesses a solid core of pitted xylem.

**Summary:** The important points arising from this ontogenetic study of the seedlings of *C. trichotomum*, which should be emphasized at present, are as follows:

1. In the case of the cotyledons and the first and second pairs of seedling leaves there are two distinct procambial strands which differentiate two annular or spiral elements, and later, at least in the lower one third of these leaves, two xylem bundles.

2. In all these leaf types the two leaf strands are associated with a unilacunar gap in the stele in both the earlier and later stages of differentiation.

3. Each of the two traces from each of the pairs of leaves examined becomes associated with an entirely separate and independent portion of the procambium and later of the vascular eustele.

4. In all cases examined the first-formed xylem of the leaf primordia, the epicotyl, cotyledons and root are discontinuous and therefore neither the protoxylem differentiating from the cotyledons nor that differentiating from the shoot are connected to, or become, the four protoxylem points of the root.

5. The transition region observed in *C. trichotomum* does not correspond with any of the transition types recorded by Van Tieghem or Sargent (1900).

6. A median protoxylem strand does not usually occur in the cotyledons. When one is present it is (1) separate from the two cotyledonary traces and their endarch protoxylem, (2) not associated with any metaxylem or phloem, and (3) stronger below and connected with the protoxylem strands which alternate with collateral bundles in the hypocotyl and extend down to form the protoxylem poles of the root. Therefore it is best interpreted as an upward extension of the protoxylem of the root, which ordinarily terminates in the hypocotyl, and is not a true cotyledonary trace. The

latter is truly double in nature and imposes on the hypocotyl its characteristic fourfold eustelic symmetry.

Further consideration of *C. trichotomum* in comparison with other types of seedlings will be included in the discussion.

## NODAL ANATOMY AND VASCULATURE OF LEAVES

**Nature and arrangement of foliar buds:** As in plants of *Syringa*, *Betula* and *Euptelea* (Garrison, 1949a, 1949b), the buds of *Clerodendron trichotomum* are of two generations; these have been designated by Garrison as "primary" and "secondary" buds for the plants mentioned above, and the same terminology has been adopted here. The term "primary" is applied to the mature buds which bear embryonic "secondary" buds in the axils of their leaf primordia.

An examination of the primary terminal and axillary buds of the young shoot of adult plants of *C. trichotomum*, shoots of two-year-old plants (with the juvenile habit), and primary buds of seedlings 4 to 6 months old, has been made. The general arrangement of buds in all these stages of development is essentially the same. In *Clerodendron trichotomum* both the terminal and axillary buds are arranged in complex groups (PLATE I:1, 2). In the axil of each leaf there is one main axillary bud, one pair of lateral accessory buds, and usually a single accessory bud below the main axillary bud (PLATE I:1, 2). Additional pairs of lateral accessory buds may be present.

Terminal and axillary buds were collected at various times during the year. In their winter condition, the terminal buds are small, dull red and extremely hairy. Between the middle of April and the beginning of May, the buds open and the new year's growth is formed. At this time many of the axillary buds grow into lateral branches also (PLATE I:1, 2). Winter buds usually consist of one or two pairs of cataphylls, and two or three pairs of leaf primordia. In the spring condition the number of leaf primordia increases giving between 6 and 12 pairs of leaf primordia.

In many cases a delay in the opening of the terminal buds has been observed and the axillary buds at the first node elongate rapidly at the beginning of the new season producing the much branched condition of the adult plants. Shortly after the new growth of terminal and axillary buds, the cataphylls (PLATE I:1) drop off (PLATE I:2); the first two foliage leaves (the transitional leaves), which are much reduced in size (PLATE I:2), are also shed after a time. The terminal and lateral branches elongate rapidly producing, in the mature plant, adult leaves (PLATE I:1, 2) and in the seedling plants (1 to 2 years old) the enlarged juvenile leaves.

**Origin, development and vascularization of buds:** During the elongation of the terminal buds, and of those axillary buds destined to become lateral branches, the leaf primordia mature into leaves. The apical meristem of such shoots retains its meristematic properties, producing the leaf primordia of a new primary bud in the late spring and summer. The



apical meristem and the production of leaf primordia and secondary buds is similar in terminal and axillary (primary) buds.

From the time of its initiation, the tissues of the first pair of minute leaf primordia and of the apical mound are all meristematic. As the second pair of leaf primordia are initiated, a small mound of meristematic tissue becomes obvious in the axil of the leaf primordia of the second node. This meristematic mound is delimited from the terminal meristematic tissues in the leaf of whose axil it occurs during the next plastochrone<sup>3</sup> by a layer of cells which are cambial-like in appearance; these form what is known as the shell-zone (Schmidt, 1924). Hence the first secondary bud is detached in primary buds in the axil of the third leaf in *Clerodendron trichotomum*. As this secondary bud assumes a position at the fourth node from the apex, it becomes more obvious due to the extensive vacuolation of surrounding cells in the cortical and pith zones. Each bud primordium which is formed in this manner has been termed a "detached meristem" (Wardlaw, 1943).

In these detached meristems during the third to fifth plastochrones of the leaves in whose axils they occur obvious procambial tissue is differentiated continuously and acropetally in connection with that in the axis, before these secondary buds produce leaf primordia. Two strands of procambium differentiate on each side of the secondary bud primordium, giving four procambial strands in all. These bud traces continue to differentiate acropetally into the first pair of leaf primordia which are produced by the secondary bud later in the season; the bud traces thus become the strands of the first pair of cataphylls.

From the time that the apical mound of meristematic tissue of a secondary bud is delimited from the meristematic tissues of the primary bud, to the elongation of the mature bud (now primary) with all of its leaf primordia, 16 or more months elapse. Detached secondary bud meristems become obvious in September or October. Both primary and secondary buds remain dormant until the following February or March, and only then are the first leaf primordia produced by the secondary bud meristem. One or two pairs of cataphylls, one pair of transitional leaves, and one or two pairs of foliage leaves are produced between March and April of this year. In March, the production of these bud primordia is preceded by marked enlargement of the bud primordia due to rapid cell division. The first pair of leaf primordia of the secondary bud develop at right angles to the subtending leaf primordium of the primary bud. Subsequent pairs of leaf primordia are initiated in an opposite and decussate arrangement. The first two or three leaf primordia thus produced become cataphylls. By the time the primary buds open and the axis starts to elongate the cataphylls and the first pairs of leaf primordia of the secondary buds

<sup>3</sup> Askenasy (1880) used this term to denote the interval of time between the appearance of two successive leaf primordia on the shoot apex. It has been used here also for successive intervals of time in the development of any one leaf primordium, viz. a leaf primordium may be 2, 3, 4, etc. plastochrones old. The interval of time for the formation of a leaf primordium is its first plastochrone.

have been produced. By September the remaining pairs of leaf primordia have been produced. These buds, now "primary," elongate the following spring.

The sequence of events in the development of primary and secondary buds of *Clerodendron trichotomum* described above is essentially the same as that observed by Garrison (1949a, 1949b) for *Syringa*, *Betula*, and *Euptelea*.

*Vascularization of buds:* Esau (1943b) has pointed out the lack of information on the development and vascularization of axillary buds, and the need for more complete investigations of this kind. She emphasizes (1953) the importance of considering vascular differentiation in both transverse and longitudinal directions, since these occur simultaneously. This investigation has been primarily concerned with the differentiation of xylem in connection with the foliar and nodal anatomy, but as far as it has been possible, procambial and phloic differentiation have also been considered. The following description of differentiation applies to both terminal and axillary buds unless otherwise stated.

*Longitudinal course of differentiation:* PROCAMBIUM. — Procambial tissue is not easily distinguished from the cells of the meristematic region and its course can only be followed with difficulty. Frequently procambium is not observed when sections are cut obliquely, or when the procambial strands themselves run obliquely at the nodes due to leaf gaps. In this study procambial tissue has been recognized by (1) its ability to stain more densely than the surrounding tissues, and (2) its narrower cells, which are elongated parallel to the long axis of the bud (cf. Esau, 1942, 1943b and 1953).

The differentiation of procambium during bud formation in *Clerodendron trichotomum* is continuous and acropetal in both primary and secondary buds. The procambium differentiates in connection with the previously existing procambium of the axis, acropetally into the leaf primordia and also into the secondary bud primordia (before they produce leaf primordia). The meristematic tissue of the apical mound and the first pair of leaf primordia is in continuity. When the production of leaf primordia is rapid, procambium does not differentiate into a pair of leaf primordia until the next plastochrone, when secondary buds are initiated in their axils. If, however, leaf primordia are initiated more slowly (at the beginning of leaf production in March and April), then procambium differentiates acropetally into the first leaf primordia during the second plastochrone. This acropetal differentiation of procambium is in accordance with procambial development in *Phlox* (Miller and Wetmore, 1946), *Linum* (Esau, 1942), *Syringa*, *Betula* and *Euptelea* (Garrison, 1949a and b).

In *Clerodendron trichotomum*, two distinct procambial strands (FIG. 6:B) differentiate into each leaf primordium during the third to fifth plastochrone after its formation. Four separate procambial strands differentiate into each secondary bud primordium (FIG. 6:B). Precocious procambial production such as described for *Linum perenne* by Esau (1942) has not been observed in *C. trichotomum*. No difference has been observed



in the differentiation of procambium to cataphylls, transitional leaves and foliage leaves.

**FIRST-FORMED PHLOEM.** — As in the seedling, the phloem is the first vascular tissue to differentiate in the vegetative buds of the mature plants of *Clerodendron trichotomum*. The first-formed phloem differentiates continuously and acropetally, following the pattern mapped out for it by the procambium. The first-formed phloem elements have been recognized in this study by their early vacuolation, loss of nuclei, thickening of the cell wall (nacré appearance) and the formation of sieve plates. Differentiation of the first-formed phloem may occur in the bases of the first leaf primordia, if production of leaf primordia is slow. During the third plastochrone of this leaf primordium, differentiation of phloem is completed (Fig. 7:B). If the production of leaf primordia is more rapid the first phloem elements can be recognized in the second pair of leaf primordia.

Two separate strands of first-formed phloem differentiate acropetally into the base of each leaf primordium, one on the abaxial surface of each procambial strand. Similarly, four strands differentiate into each secondary bud primordium, about the time that the first pair of leaf primordia are produced in that bud. The first-formed phloem elements differentiate to the base of each of the first pair of leaves, so providing the bud primordium with a vascular connection to the main axis.

**FIRST-FORMED XYLEM.** — The first-formed xylem elements differentiate considerably later than the first-formed phloem elements. The timing of their differentiation is extremely variable and is connected with the rate at which leaf primordia are produced. If production of leaf primordia is slow, some xylem may be produced in a leaf primordium during its third plastochrone (Figs. 6:B, 7:B). However, during more rapid production of leaf primordia the first xylem elements may not be differentiated in a leaf primordium until its fourth or fifth plastochrone. In either case, differentiation of the first-formed xylem elements is by-directional and discontinuous. A strand of first-formed xylem appears on the adaxial side of each of the two procambial strands; these xylem elements were recognized by the use of the criteria Esau has cited (1942). They are initiated at the base or some distance above the base in the leaf primordium. In either case differentiation occurs in two directions simultaneously, viz. acropetally towards the tip of the leaf primordium, and basipetally towards the main axis of the bud. The basipetally differentiating first xylem elements meet and join with acropetally differentiating first-formed xylem in the main axis of the bud. The actual union of these traces does not occur until about the fifth plastochrone of the leaf primordium in whose axil the bud occurs (Figs. 6:B, 7:B).

Differentiation of the first xylem elements in the secondary bud primordia does not occur until the fifth plasochrone of the leaf in whose axil it occurs although mature phloem may be present much earlier. A secondary bud at this time has two or three pairs of leaf primordia, into which the procambium and phloem have already developed acropetally, as described above. The first xylem elements differentiate acropetally into the base of

the secondary bud in continuity with the xylem trace to the subtending leaf primordium of the primary bud. Subsequently, in the secondary bud itself, the first xylem elements to differentiate are observed, as in the primary buds, at or near the base of the third or fourth pair of leaf primordia. Further differentiation is as described for the primary buds.

*Transverse course of differentiation: PROCAMBIUM.* — The first procam-

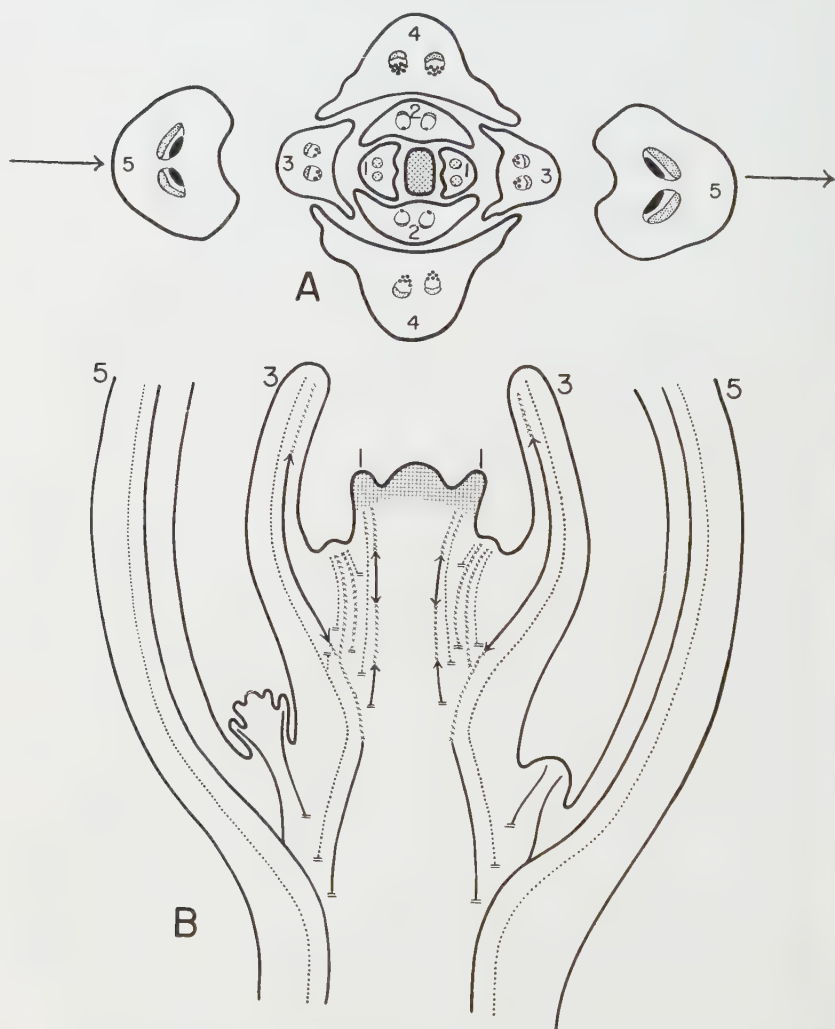


FIGURE 6

THE COURSE OF VASCULAR DIFFERENTIATION IN THE FIRST, THIRD AND FIFTH LEAF PRIMORDIA OF A BUD OF *Clerodendron trichotomum*. Crosses indicate the procambial strands. Phloem is shown as a dotted line. Xylem is represented as a solid black line. The arrows indicate the direction of differentiation. Traces terminating in a pair of transverse lines pass out of the plane of section.



bium differentiates in the main axis below the youngest pair of leaf primordia. In transverse sections it appears as four small groups of densely staining cells, these represent the four procambial traces to the youngest pair of leaves (two strands to each leaf). At this level they appear to be linked laterally by cells with stain-ability intermediate between procambium and ground tissue. These cells constitute what has been termed "less determined meristematic tissue," and will become parenchyma of the interfasc-

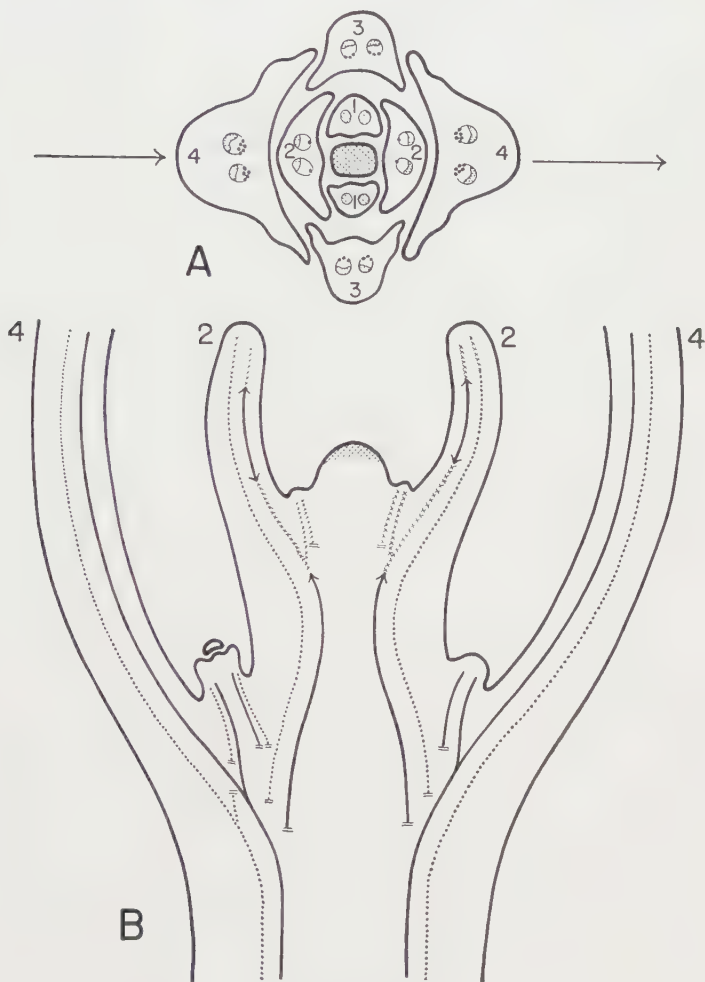


FIGURE 7

THE COURSE OF VASCULAR DIFFERENTIATION IN THE SECOND AND FOURTH LEAF PRIMORDIA OF A BUD OF *Clerodendron trichotomum*. Symbols are the same as in figure 6.

cicular regions and leaf gaps (cf. Esau, 1943b and 1953). The nests of procambium in the main axis divide both anticlinally and periclinally, so building up the four distinct groups in the main axis.

**FIRST-FORMED PHLOEM.** — The acropetally differentiating first-formed phloem appears in the main axis below the youngest node, and in the second pair of leaf primordia. Its differentiation is initiated on the outside of the axis procambial trace and on the abaxial surface of each of the procambial strands to the leaf primordia (FIG. 6:A, 6:B). Subsequent development of the first-formed phloem is centripetal; laterally it develops in advance of the first-formed xylem elements (FIG. 6:A).

**FIRST-FORMED XYLEM.** — In the second or third pair of leaf primordia some distance from their point of origin on the main axis, one xylem element differentiates in a median position, on the adaxial surface of each of the two procambial strands. Subsequent differentiation from these first-formed xylem elements is centrifugal in direction. Their lateral spread lags behind that of the first differentiated phloem elements.

The direction of differentiation of procambium, of the first-formed phloem, and of the first-formed xylem elements in *Clerodendron trichotomum* corresponds to that recorded by Esau for *Linum* (1942, 1943a), *Helianthus* and *Sambucus* (1945) (cf. also Esau 1943b and 1954); by Miller and Wetmore for *Phlox* (1946); Garrison for *Syringa* (1949a), *Betula* and *Euptelea* (1949b); and in *Ginkgo* (Gunckel and Wetmore, 1946a and 1946b), *Sequoia* (Sterling, 1945) and *Pseudotsuga* (Sterling, 1947) at least in a transverse direction.

**Vascularization of node and internode:** Serial sections of primary terminal buds of mature plants, and of four-month-old seedlings have been studied for the initial stages in the vascularization of the main axis. It has not always been possible to follow, in these stages, the course of each foliar strand. For this reason, the nodal structure in the mature two-year-old plant is also described. Thus, as complete a picture as possible of the nodal anatomy of *Clerodendron trichotomum* is given.

**Vascularization of nodes and internodes in terminal buds:** Serial sections of terminal buds of both adult and seedling plants show identical nodal conditions. For the purpose of simplicity in the following description, bud traces are not considered, but will be discussed in connection with the mature nodal anatomy. The following description is made from the fifth node of a terminal bud upwards towards the apical meristem (FIG. 8). Below the fifth node secondary activity complicates the nodal anatomy.

In the internodal region below the fifth node, six pairs of vascular strands are present. These have been designated as A, B, and C (FIG. 8:1). At a slightly higher level, it appears that the four B strands are double in nature. The A and C strands move apart forming an obvious gap in the eustele as the fifth node is approached, and at this node, the two pairs of A traces pass out to the fifth pair of leaves (from the apical meristem) (FIG. 8:2). At this level also the lens-shaped axillary bud primordia constrict the stele pushing the B and C pairs to the opposite side of the stele, and now four new small strands, D, separate from the two pairs of B

strands. The node, then, at this level, still contains six pairs of vascular strands (FIG. 8:2, 3).

In the internode above the fifth node, the eustele closes and the six

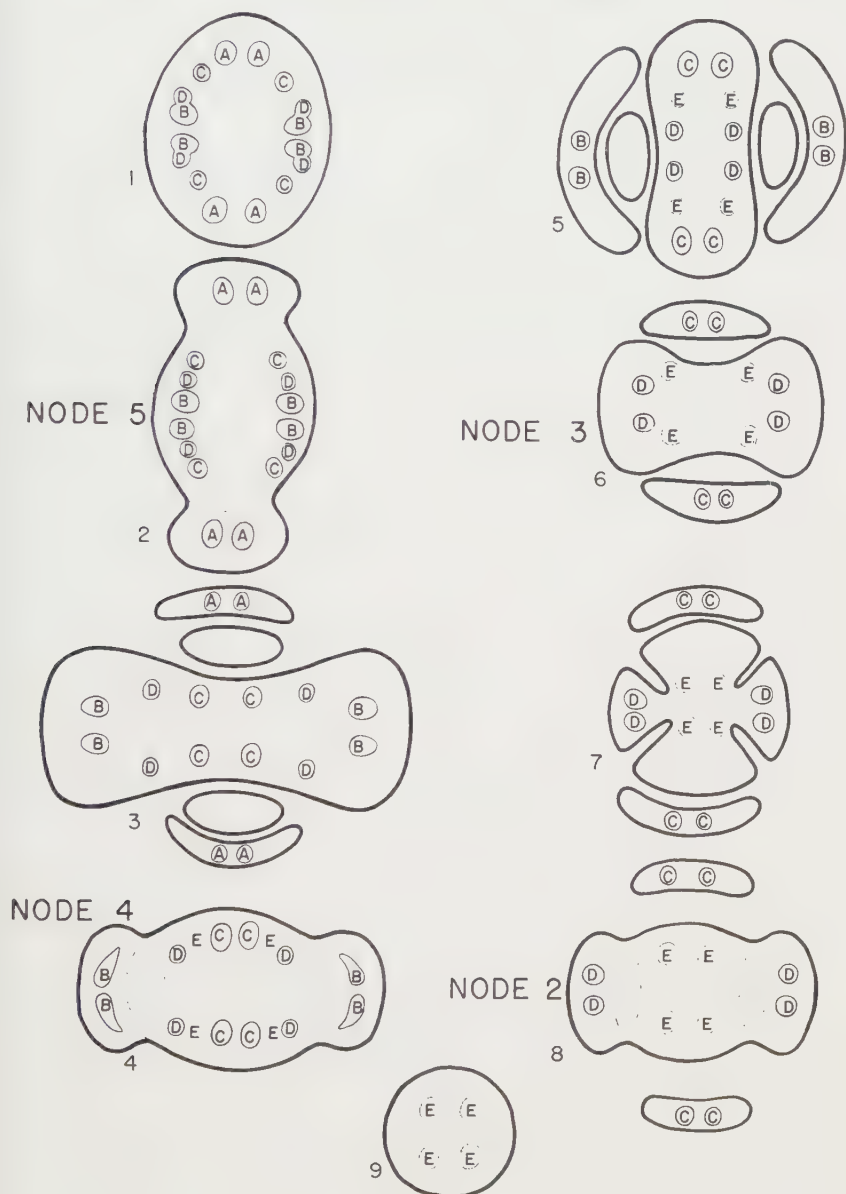


FIGURE 8

A SERIES OF SECTIONS THROUGH THE PRIMARY TERMINAL BUD OF *Clerodendron trichotomum*. Explanation in text.



pairs of strands resume a symmetrical arrangement. The fifth pair of leaves has detached from the axis and each contains two A strands. As the fourth node is approached the B and D pairs separate at either end of the stele, and the two pairs of B traces pass out to the leaves. Again, the axillary bud primordia at the fourth node constrict the stele, and the C and D strand pairs are pushed out of position. Some distance above, where the normal symmetry returns, six pairs of strands are present. The C and D bundle pairs are obvious although there are fewer xylem elements than in the internode below. The four new strands (E) are inconspicuous and procambial (FIG. 8:4). Their origin is uncertain and it may be that at the fourth node they split off obliquely and so were not observed.

From a study of the mature nodal structure, and of the fifth node (cf. above) it is probable that these procambial strands (E) originate from the C traces at the fourth node. However, these procambial strands appear more obvious and stronger in the nodal and internodal regions above. It may be that such a condition could account for the basipetal differentiation of procambium in foliar traces reported by some workers, e.g. Foster, 1935; Kaplan, 1937; Grégoire, 1938; Boke, 1940, etc. However, in the present case the procambial bundle E may run an oblique course and so escape observation where it attaches to the strand C. At higher levels procambium has been observed always to differentiate acropetally into each leaf primordium in continuity with the procambium in the main axis. It has not been possible to observe the course of differentiation of the strand E at its base.

The vascular traces which pass out to the leaves are stronger at the nodes where they depart, than at any other level in the axis. Such a condition would be provided for by the stronger development of procambium strands above the region of their origin.

In the fourth internode there are, then, four distinct pairs of xylem strands (C and D), and two pairs of less distinct procambial strands (E). At the third node the two pairs of leaf traces, C, pass out to the pair of leaves directly above those at the fifth node, and at right angles to the traces passing out at the fourth node (FIG. 8:5, 6). It should be emphasized that the A traces were replaced in position by the C strands, and that the C traces themselves are replaced in position by the procambial strands, E.

At node 2, the two pairs of D traces pass out to the second pair of leaves (FIG. 8:7, 8), i.e. four nodes above their origin from the B strands. Only the four procambial groups (E), now much more conspicuous, remain in the internode above (FIG. 8:9). These pass out at the first node to the youngest pair of leaves.

It appears, then, that opposite pairs of leaves are supplied by separate vascular systems of the stele. That is, the vascular system supplying traces to the pairs of leaves at the fifth, third and first nodes (A, C, and E, respectively) are quite separate from the system supplying leaves at the fourth and second nodes (B and D, respectively). In fact, each leaf in

a separate phyllotactic position is supplied by two quite separate strands in the eustele.

In each case it appears that the traces for any one pair of leaves originate as vascular strands of the eustele at one node, pass upwards through two nodes, and depart to the pair of leaves at the next node above. For example, at the fifth node the D strands arise from the B traces; at the fourth node the B traces pass out; at the second node the D traces pass out.

*Vascular structure at the node in adult plants:* The nodal and internodal conditions in the adult plant are comparable with those described above, except that secondary tissue has been added. In this condition the vascular strands described above have been identified by their primary xylem groups which project into the pith. At each internode twelve such primary xylem masses can be recognized. Eight of these are always more obvious; these are the strands which will become foliar traces at the next two nodes above. The four smaller primary xylem groups are those which separated, at the node below, from the two pairs of leaf traces which will depart at the node immediately above.

The series of diagrams in figures 9 and 10 illustrates this condition at three successive nodes, A, B and C. Only the primary xylem groups are shown here. At node A, the traces marked 1 depart to the pair of leaves at this node. In near nodal sections the stele separates to form a single gap through which the traces gradually move outwards towards the leaf base; successive pairs of strands become detached from this, and pass into the base of the petiole. Three or four pairs of strands pass out to the leaf from these two separate groups (1) in the axis (FIG. 9). Finally the two traces (1) completely detach themselves from the stele and remain separated from it by parenchyma. At this stage, two bud traces are detached at each side of the axis, from the same traces that supply the leaves, and pass out obliquely to the axillary buds. The vasculature of accessory buds has not been followed in this study. Finally the remainder of strand 1 passes out laterally to vascularize the wings of the petiole as shown in figure 14.

At the same time that the bud traces become detached, two small pairs of primary xylem groups (4) separate from the sides of the larger xylem groups (2) (i.e. in the direction of the departing strands, see FIG. 9) which will depart at the node above (B). In the internode above, the stele again has twelve groups of primary xylem. The four smaller groups (3) (FIG. 9), of the internode below node A, now enlarge considerably and move to close the gap made in the stele by the departing strands (1). Now the eight larger primary xylem groups (3 and 2) are again in opposite positions (FIG. 9).

Similarly, at node B, the four strands, numbered 2, depart through a unilacunar gap in the stele in a similar manner. The number of primary xylem groups is again renewed by the larger traces (3) detaching four small primary groups (5) (FIG. 9). The smaller groups, numbered 4, in-

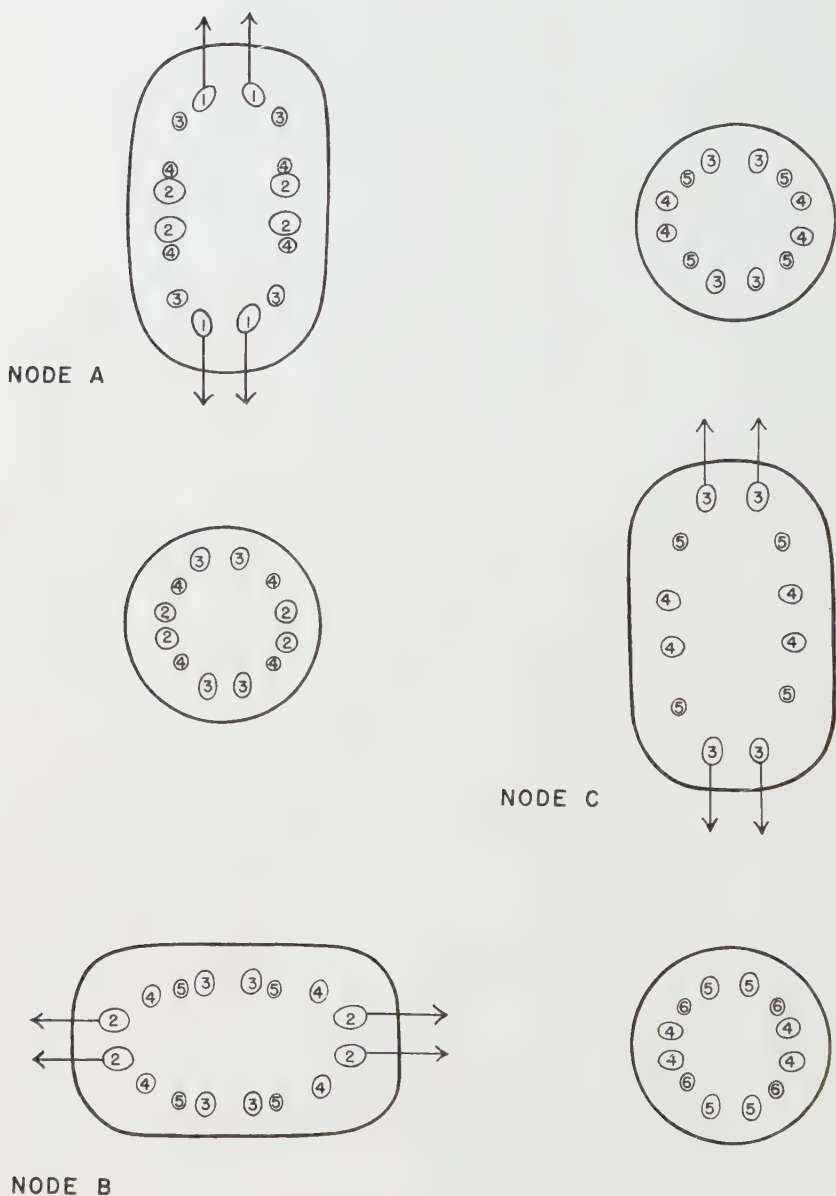


FIGURE 9

DIAGRAMMATIC SERIES THROUGH THE ADULT NODE OF *C. trichotomum*. Explanation in text.



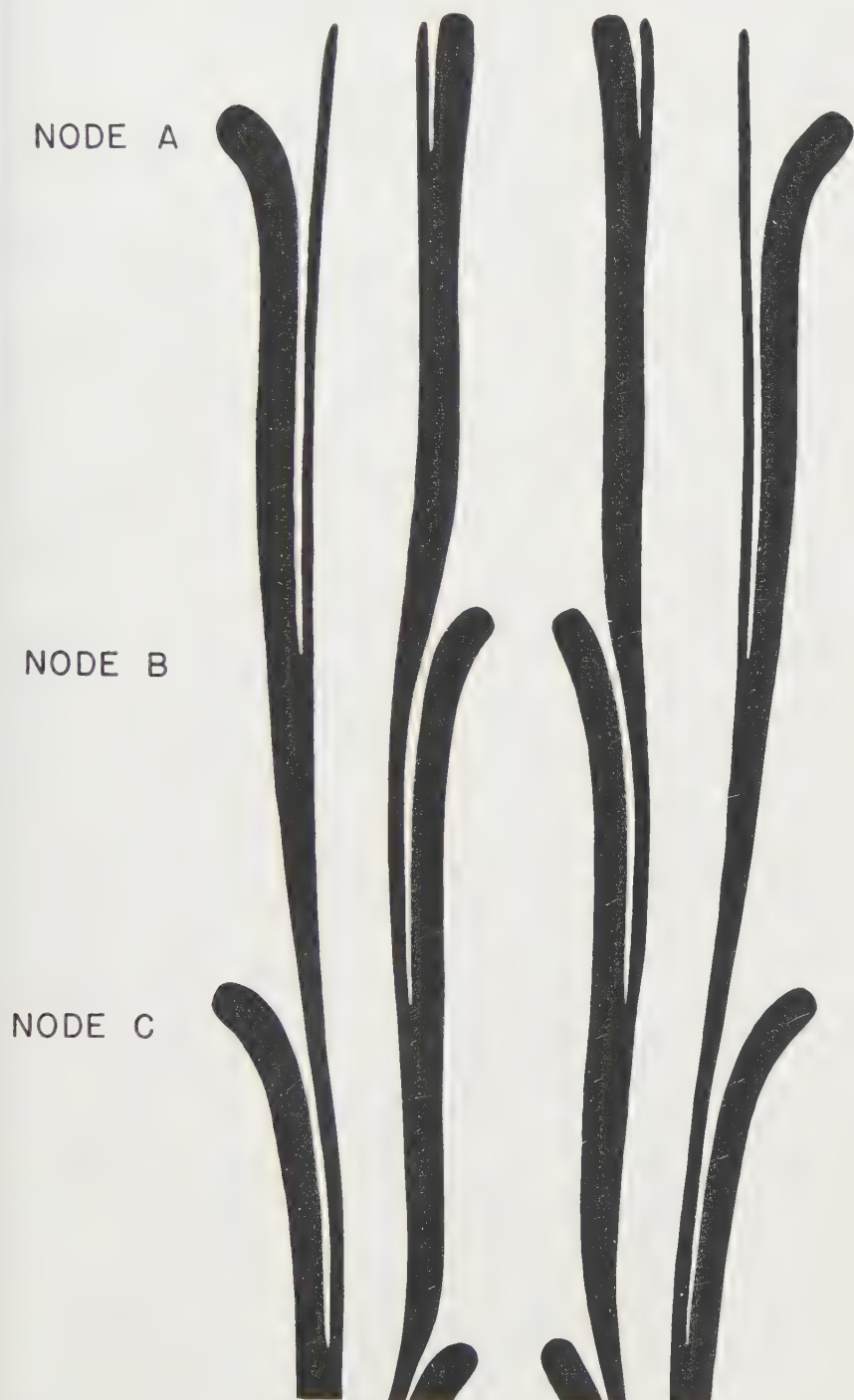


FIGURE 10

THE LONGITUDINAL COURSE OF THE PRIMARY VASCULAR STRANDS IN THE STEM OF *Clerodendron trichotomum*. Only the vascular strands on the near side of the stem are shown.

crease in size and move into the position of the departing strands to close the unilacunar gap in the internode above B.

The traces, numbered 3, depart at node C and two more groups of primary xylem (6) detach themselves from the enlarged groups (4) (FIG. 9). At the node above C, the traces numbered 4, which originated four nodes below at node A, from traces 2, will depart to the pair of leaves in the same phyllotactic position as those supplied by the traces 2.

In *Clerodendron trichotomum*, where the phyllotaxy is decussate, each leaf is vascularized by two discrete strands that are related to a single gap in the stele. The vascular strands supplying the leaves at alternate nodes arise from independent systems. These systems are only linked laterally by the production of secondary tissue which is not concerned in the foliar supply. The leaves are vascularized from an eight-strand system: the primary vascularization is a system of eight independent strands, consisting of four pairs which independently supply the pairs of traces to leaves in the four phyllotactic positions.

*Comparison of Clerodendron trichotomum with other plants possessing a similar nodal anatomy:* Several plants possessing a similar unilacunar, double trace condition have been examined. These are described briefly below.

(1) *Ephedra* (By examination of stem tip serial sections supplied by Dr. Taylor A. Steeves, Harvard University) (FIG. 11).

As in *C. trichotomum*, the leaves of *Ephedra* are vascularized by two discrete traces which depart from the eustele through a unilacunar gap. In the slides of *Ephedra* examined, the leaves, as in *C. trichotomum*, possess a decussate phyllotaxy, but, unlike *C. trichotomum*, the scale-like leaves have a sheathing base.

Each internode contains eight bundles in its primary vascular condition (FIG. 11); two pairs of large bundles alternate with two pairs of small ones. At node 1, the two smaller pairs of traces, A, depart through a single gap in the stele (FIG. 11), and the two remaining pairs of bundles (B) branch to form two additional pairs of bundles (C). These two bundles (C) run through one node above (node 2) where these produce two further pairs of bundles (D), and then depart to the pair of leaves at the next node above (node 3). Meanwhile, the two original bundles (now leaf traces B) supply the leaves at node 2 (FIG. 11).

The leaves of *Ephedra* are therefore vascularized at successive nodes from a four-strand system. Each of these four strands supply one of the pair of leaves at every node.

(2) *Austrobaileya scandens* (From examination of serial sections through the terminal bud, first and second nodes of a young shoot. Material from the Harvard University Wood Collection; H-27800, Brass 18160.)

In *Austrobaileya*, as in *C. trichotomum*, the leaves are vascularized by two pairs of strands, through a unilacunar gap in the eustele. Moreover, these arise from two separate procambial strands, although during later stages in differentiation of vascular tissues the strands may appear to

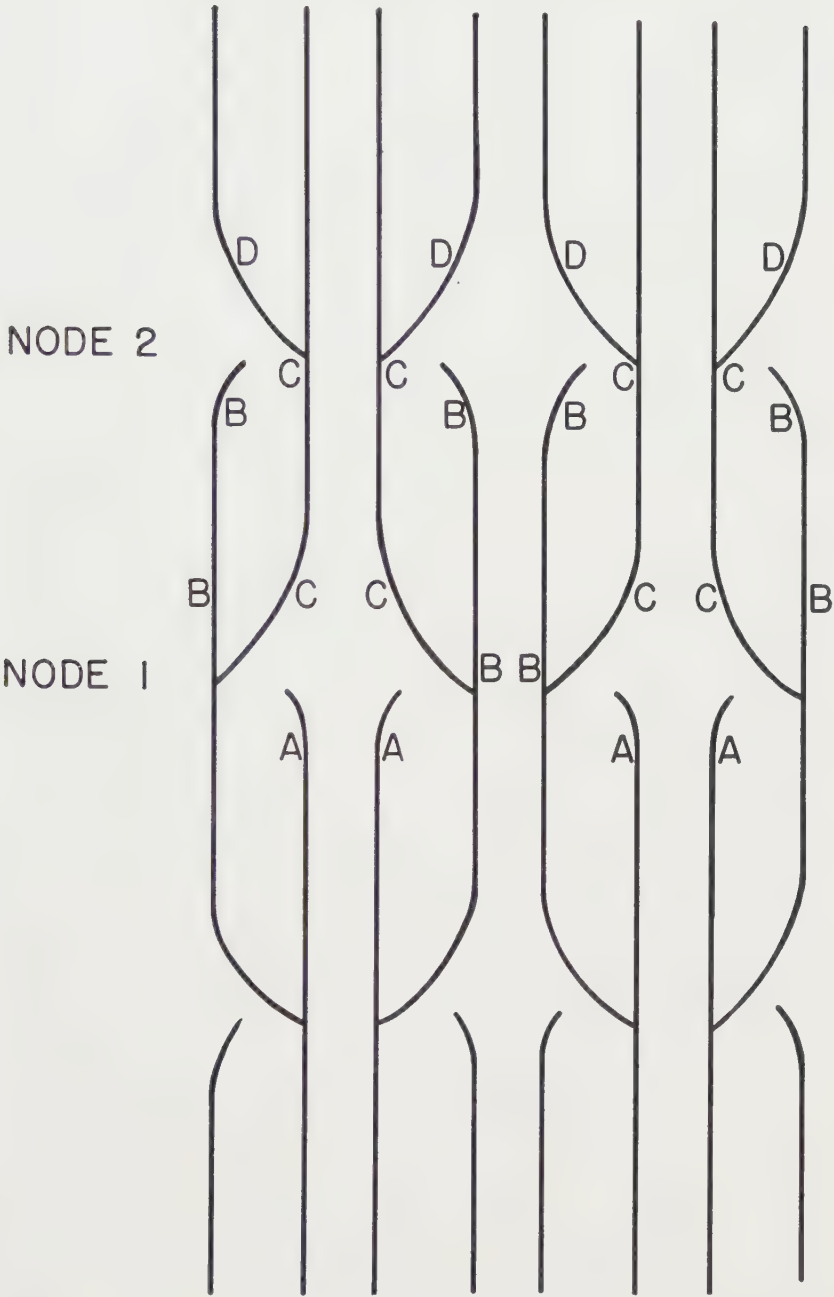


FIGURE 11

THE LONGITUDINAL COURSE OF THE PRIMARY VASCULAR STRANDS IN THE STEM OF *Ephedra*, AS IF SPREAD OUT IN ONE PLANE.



approximate (Bailey and Swamy, 1949). Below the node, the two foliar traces remain independent from one another and arise from two different strands of the eustele. In the young portions of the plant, the phyllotaxy is typically decussate.

As in *Ephedra*, the leaves are vascularized by a four-strand system. This condition is obscured at the first and second nodes by secondary activity. Below the nodes, the four strands supplying the leaves separate into twelve pairs of traces and run with the four-strand system for some distance before passing out to the leaves. However, at each node in the terminal bud, each of the four strands divides to give a trace which will pass out to one of the leaves at the node above (FIG. 12). Therefore, each strand supplies half the vascularization of one leaf at successive nodes, and not, as in *Clerodendron trichotomum*, one leaf only at alternate nodes.

(3) *Trimenia weinmanniaefolia* (From examination of serial sections of the stem through several successive nodes. Material from the Harvard University Wood Collection, H-27965.)

In *Trimenia*, a four-strand vascular system supplies the decussately arranged leaves at each node with four traces (FIG. 13), as in *Austrobaileya* and *Ephedra*. A unilacunar gap is formed in the eustele through which two distinct strands depart to the leaf. However, unlike the condition in *Clerodendron trichotomum*, at each node one of the four strands supplies one of the traces to each leaf (FIG. 13).

A similar condition to that observed in *Ephedra*, *Austrobaileya* and *Trimenia* has been recorded for *Ascarina*, *Hedyosmum* and *Chloranthus* (Swamy, 1953a). *Hedyosmum* and *Chloranthus* show a modification in the division of the foliar traces, however, but possess a four-strand eustelic condition in the stem comparable with that described above for *Ephedra*, *Austrobaileya* and *Trimenia*.

It is evident from the above comparisons that although the leaves of *Austrobaileya* (Bailey and Swamy, 1949), *Trimenia* (Money, Bailey and Swamy, 1950), *Ascarina*, *Hedyosmum* and *Chloranthus* (Swamy and Bailey, 1950; Swamy, 1953a) are vascularized by "two discrete traces arising from two entirely independent parts of the eustele," the strands vascularizing the leaves of *Clerodendron trichotomum* arise from even more independent strands in the stele. In the latter case two quite separate vascular systems are present in the stele, and any one strand supplies the vasculature of leaves in one phyllotactic position only. Four strands supply the leaves at one node, and four entirely separate strands supply the foliar traces at the node above.

**Vascularization of vegetative leaves, and comparison with other leaf types:** *Adult vegetative leaves—development:* The origin and initial vascularization of leaf primordia has already been discussed in relation to the development of buds. Soon after the production of leaf primordia, and during the third and fourth plastochrones, the marginal and submarginal initials are formed. The subsequent development of these embryonic layers is similar to that described in detail by Esau (1953, pp. 442–447) for ordinary dicotyledonous leaves having an expanded blade,

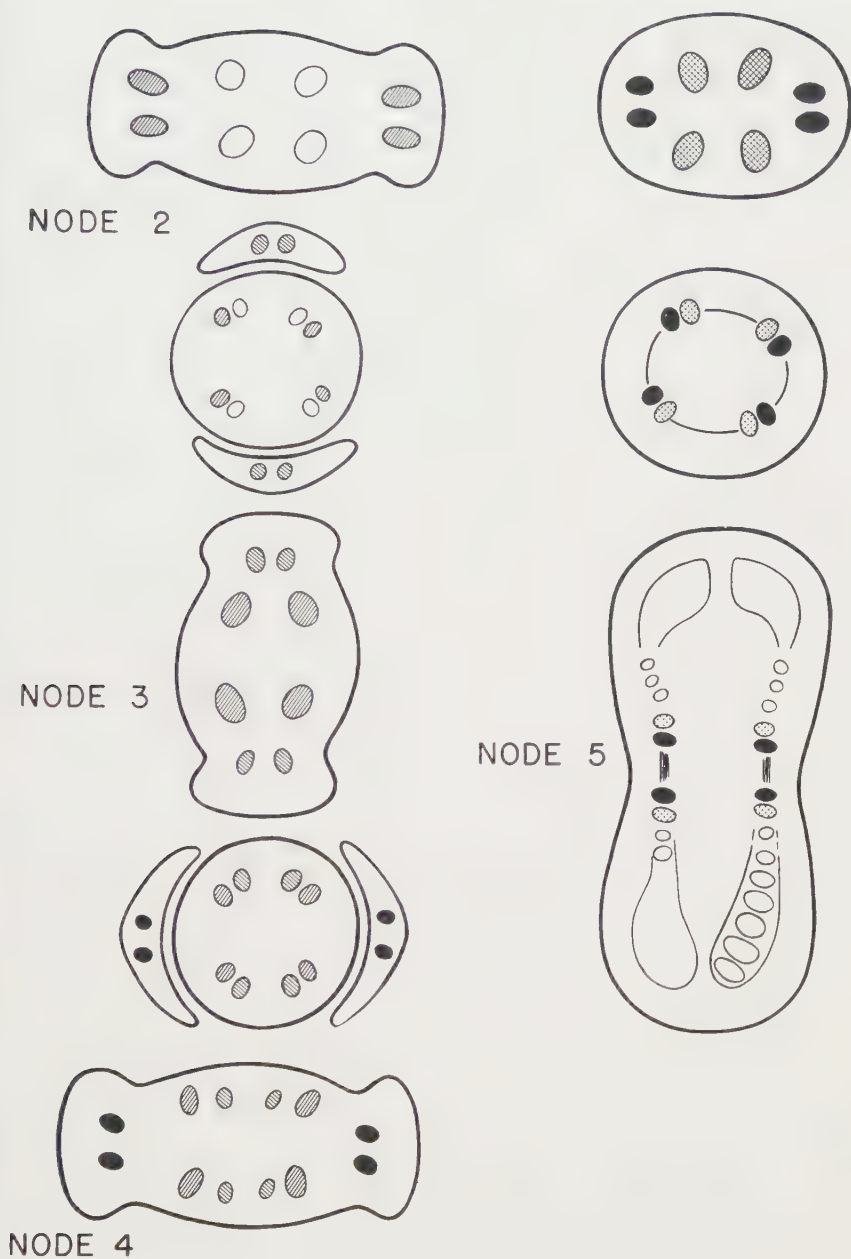


FIGURE 12  
THE NODAL ANATOMY OF *Austrobaileya*.

and a petiole, and is comparable with the development of tissues in leaves of *Nicotiana tabacum* (Avery, 1933; Foster, 1936). The details of their development will therefore not be described here.

However, in *Clerodendron trichotomum*, two distinct procambial strands differentiate acropetally into the developing leaf primordia. The vascular pattern is mapped out at an early stage by further procambial differentiation, and each of the two strands is extended to form the procambial

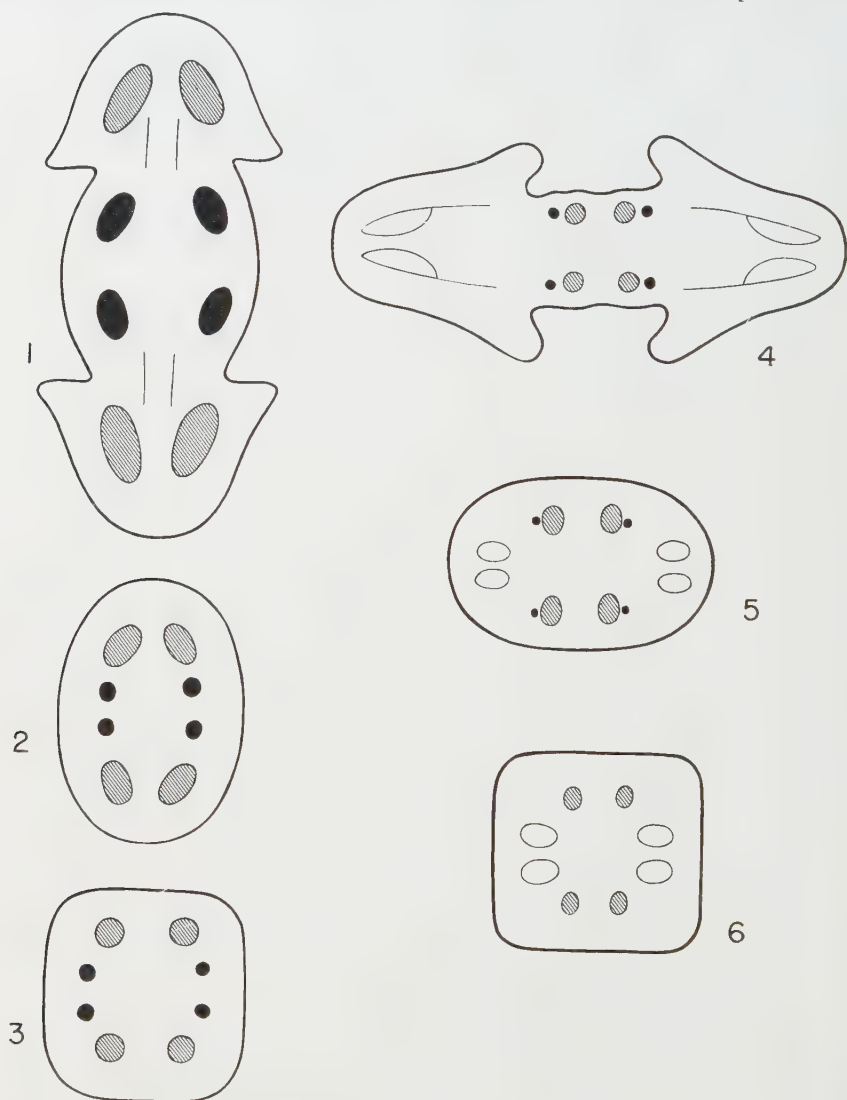


FIGURE 13  
THE NODAL ANATOMY OF *Trimenia*.



network of half the leaf. The first vascular tissue to differentiate in the leaves is phloem, and this develops acropetally in continuity with the existing first-formed phloem in the axis. The first phloem is formed in the leaf during its first or second plastochrone. The first xylem elements usually differentiate in a leaf during its fourth or fifth plastochrone. The differentiation of xylem first occurs at the base of the leaf primordium, and is bidirectional and discontinuous. Differentiation of late-formed primary xylem and phloem has not been studied.

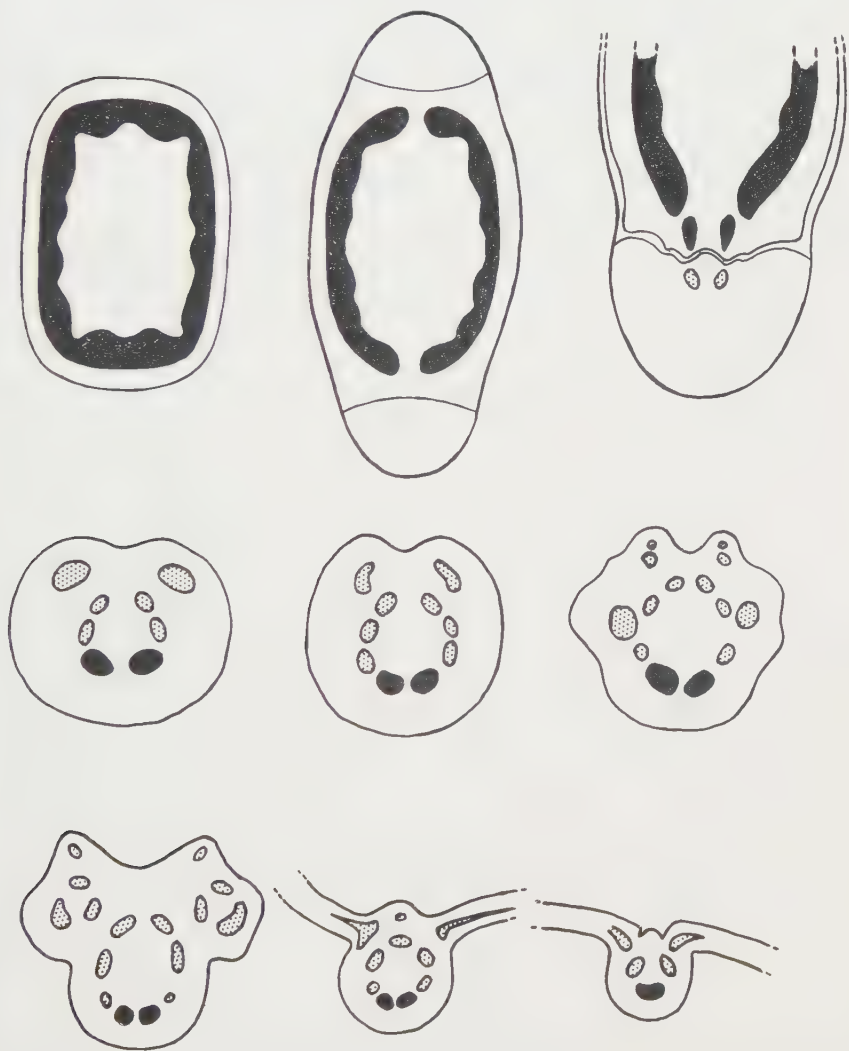


FIGURE 14

A SERIES OF SECTIONS THROUGH THE NODE AND LEAF OF *Clerodendron trichotomum*.

*Mature adult leaf — vasculature:* In the mature leaf the two leaf traces divide before departing through a unilacunar gap in the stele. The main traces divide to form three or four pairs of subsidiary strands and a pair of bud traces, and finally depart to the base of the petiole. The first two traces to depart to the leaf base form the main strands (shown in black in FIG. 14) of the mid-rib, and these remain distinct throughout the petiole and mid-rib of the lamina, until finally they approximate towards the leaf apex (FIG. 14). The last two strands departing through the single gap in the stele, vascularize the wings of the petiole (FIG. 14). The series of sections shown in figure 14 illustrates the course of the foliar strands through the petiole and mid-rib of the lamina. Throughout the petiole and lower portion of the mid-rib the bilaterally symmetrical arrangement is evident; towards the leaf tip, the number of strands decreases and fusion of the median strands frequently occurs. In many of the cleared specimens examined, the two median strands remained distinct for the entire length of the mid-rib; in some cases, however, fusion occurred towards the tip of the leaf.

**Comparison of vasculature of adult and other leaf types:** *Juvenile leaves:* Apart from the much larger size of the juvenile leaves, their vascular pattern is essentially the same as that of the adult leaves. They are also vascularized by two discrete foliar strands, which subdivide as described for the adult leaf form. The two median strands which run through the mid-rib of the leaf may also merge towards the tip of the juvenile leaves.

*Floral bracts:* The bracts which subtend the trichotomous divisions of the floral axis are vascularized by two strands which arise in a similar manner to those which supply the ordinary vegetative leaves. These strands also depart through a unilacunar gap in the stele. In cleared specimens, the strands remain distinct and each appears to consist of one spiral and two or more scalariform elements (FIG. 15). The bract traces arise from an eight-strand system in a similar manner to that already described for the foliage leaves.

Just below the node where the trichotomy of the floral axis occurs, the two pairs of bract traces become obvious. At about the level where the bract traces separate from the stele, other divisions appear in the vascular cylinder (FIG. 16). These are the regions where the main stele divides to produce three separate vascular cylinders, one for each of the divisions of the trichotomy of the floral axis. The bract strands now depart to the base of the bracts, and these may divide to produce one pair of lateral strands as they do so (FIG. 16). After the two pairs of traces leave the stele, the unilacunar gaps close, forming a horseshoe-shaped vascular cylinder at either end of the elongated axis (FIG. 16) with a third vascular cylinder, medianly placed, which is open at either end (FIG. 16). Constrictions now form in the axis, and all three future floral axis steles become closed. Finally, the stem itself divides into three floral branches (FIG. 16).

In all the cleared specimens of bracts which have been examined, the two median strands remain distinct throughout their length. They do not

appear to merge towards the tip of the bracts, as is sometimes the case in the foliage leaves. The bracts differ from the foliage leaves in their reduced size and narrowly ovate shape. Their vascularization, however, is similar in that they are supplied by two discrete traces through a unilacunar gap in the stele.

*Cataphylls:* The vascularization of the bud scales has already been discussed earlier in this chapter in connection with leaf primordia. As in the vegetative leaves, and bract scales, the cataphylls are supplied by two separate procambial traces, which arise from the eight-strand system in the same way as the ordinary foliar traces. The subsequent development of the cataphylls is similar to that described by Esau (1953). The vasculature of the cataphylls of *Clerodendron trichotomum* appears, as in the floral bracts, to be limited to the two median strands with occasionally one pair of smaller lateral strands. The cataphylls and floral bracts drop off shortly after the primary vegetative and floral buds elongate.

*Transitional leaves:* In *C. trichotomum* each bud usually possesses one pair of transitional leaves, just above the cataphylls, which have a more expanded lamina, are green, and lack the great abundance of hairs and cells containing phenolic compounds found in the bud scales. They are, however, reduced in size and transitional in shape between the bud scales and adult foliage leaves. Like the cataphylls and floral bracts, they are shed shortly after the primary buds open. The transitional leaves are supplied with two discrete traces through a single gap in the stele. These traces arise from the eight-strand stelar system in a similar manner to those supplying the foliage leaves and bud scales. However, in the transitional leaves two pairs of laterals are usually produced by the main strands; these latter strands may approximate towards the transitional leaf apex, as in the case of the regular foliage leaves. Hence all these leaf types, the adult and the juvenile foliage leaves, the floral bracts, cataphylls and transitional leaves are similar in their vascularization.

*Cotyledons:* The vascularization of the cotyledons was discussed earlier. These also are supplied with two discrete strands, although the condition at the cotyledonary node differs from the nodes of the epicotyl. However, the two cotyledonary traces do arise from two separate procambial strands, as is the case in the foliage leaves, cataphylls, transitional leaves and floral bracts.

Considering all the leaf types mentioned above, it is apparent that the vascular supply in all these cases is comparable. Each leaf, regardless of size and form, is vascularized by two discrete strands. In adult and juvenile leaves, in floral bracts, cataphylls and transitional leaves, these two traces arise from the eight-strand stelar system in the same manner, and depart to the leaves, in each case, through a unilacunar gap in the stele. In all six types of foliar appendages the two vascular strands differentiate from two discrete procambial strands in a comparable manner. Hence these leaf types are basically the same and have been modified according to their position and function in relation to the other parts of the plant.

*The initiation of an eight-strand vascular system in the seedling:* In the



seedling of *Clerodendron trichotomum* there is a four-strand system at the cotyledonary node, which is comparable to the situation observed in adult plants of *Austrobaileya*, *Trimenia* and *Ephedra*. However, in *C. trichotomum*, the cotyledonary traces pass out to the cotyledons directly at their node of origin, and not one node above as in the species mentioned above.

Examination of the epicotyl in seedlings of *Clerodendron* with one pair of leaves only, also demonstrates a four-strand condition. But, between

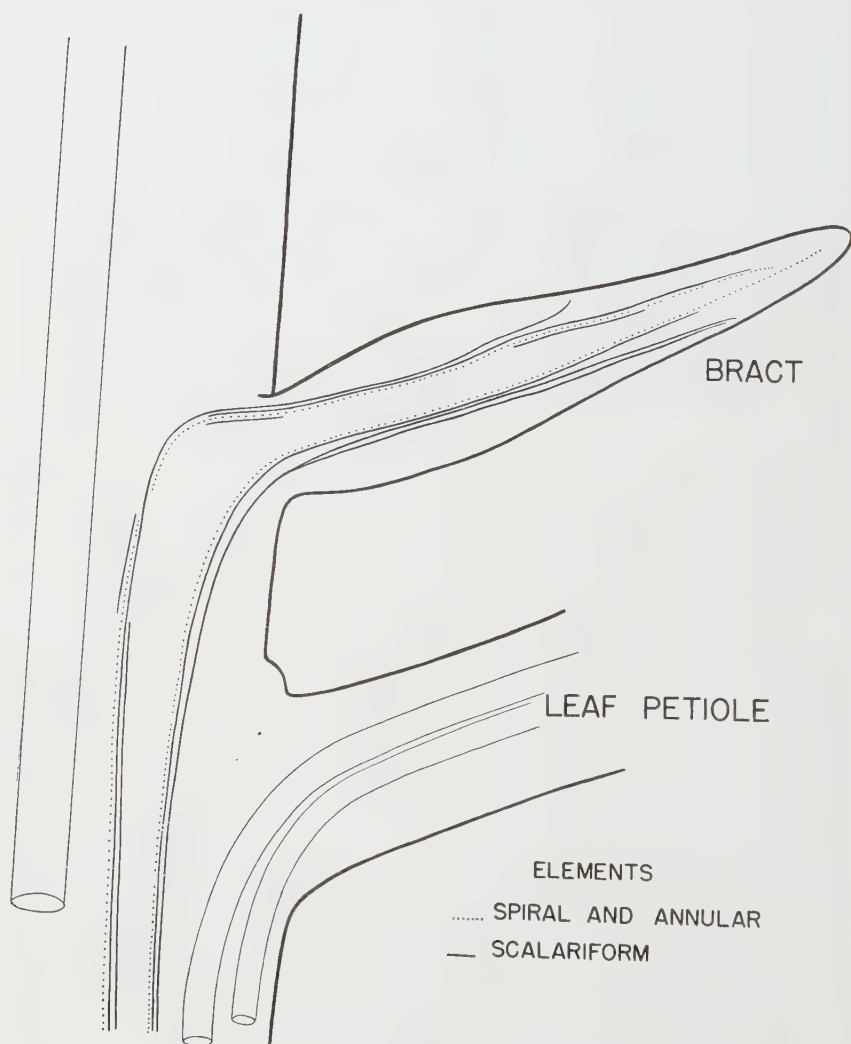


FIGURE 15

DIAGRAM OF A CLEARED FLORAL BRACT SHOWING THE XYLEM ELEMENTS.  
(*Clerodendron trichotomum*)

the four first-formed xylem groups of the first pair of leaves, four additional xylem groups differentiate from the next pair of leaf primordia which are produced, so forming the eight-strand system apparent in the adult plant. The xylem of the second group of foliar traces differentiates basipetally down the entire length of the epicotyl to join the late-formed xylem just above the cotyledonary node. There is some variation in the position of attachment of the second group of foliar traces, but in all cases they attach to the late-formed primary xylem between the cotyledonary node, and approximately 1000 micra above. Seedlings with more than two pairs of leaf primordia were not examined and it is therefore not possible to say how the traces to the third pair of leaf primordia arose without further investigation. Foliar traces to subsequent leaf primordia have not been observed in older seedlings in the epicotyl below the first pair of leaf

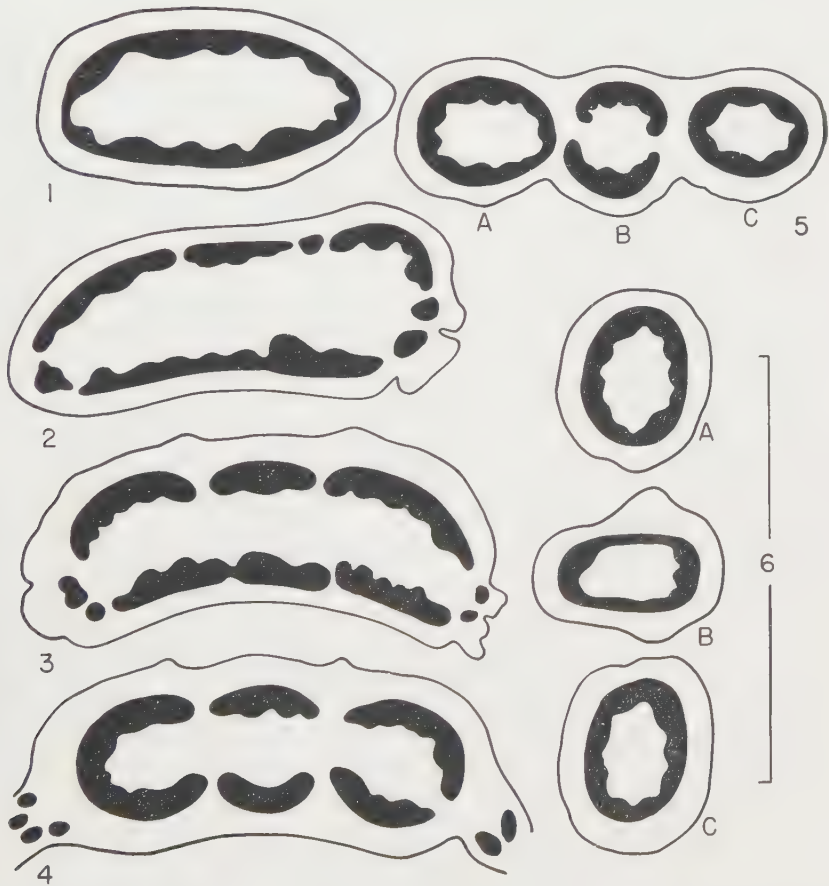


FIGURE 16

A SERIES OF SECTIONS THROUGH THE FLORAL TRICHOTOMY OF *C. trichotomum*, SHOWING THE DEPARTURE OF THE BRACT TRACES.

primordia, and traces to the third pair of leaves may have arisen at the first-formed node from the foliar traces to this pair of leaves.

**Summary:** (1) In the primary buds: (a) two separate procambial strands differentiate continuously and acropetally into each leaf primordium during the first and second plastochrones. (b) First-formed phloem similarly differentiates acropetally during the second plastochrone. The phloem differentiates first on the abaxial surface of each procambial strand and spreads centripetally. (c) The first-formed xylem differentiates discontinuously (both acropetally and basipetally, simultaneously) during the third and fourth plastochrones, on the adaxial surface of each procambial strand and spreads in a centrifugal direction.

(2) The secondary buds are formed from "detached meristems" during the third plastochrone; differentiation of vascular tissues occurs in a similar manner to that in the primary buds.

(3) An eight-bundle eustelic condition develops in the node; four of these supply foliar traces to the leaves at one node, and four quite separate and independent bundles supply the leaves alternating with these at the node above, i.e. there are two independent systems supplying pairs of leaves at alternate nodes.

(4) Each pair of foliar traces arises at one node, passes upwards through two nodes and departs through a unilacunar gap in the stele to the leaves at the next node above.

(5) All the different types of foliar appendages examined in *Clerodendron trichotomum*, viz. adult leaves, juvenile leaves, cataphylls, transitional leaves, floral bracts (and also cotyledons and the first pair of seedling leaves), are vascularized by two discrete traces which depart through a single gap in the primary stele.

(6) These foliar traces in all cases differentiate from two separate procambial strands, and arise (except to the cotyledons) from two entirely independent bundles of the eight-strand eustele.

(7) The examination of nodal material of *Austrobaileya*, *Trimenia* and *Ephedra* has shown that the leaves in all these plants are vascularized by two discrete traces which arise independently from a four-strand primary stele. The foliar traces in all cases have arisen from two separate procambial strands.

(8) The eight-strand vascular system in adult plants of *Clerodendron trichotomum* has arisen by the basipetal differentiation of the foliar traces of the first two pairs of seedling leaves. Thus, a four-strand, and then an eight-strand system is formed in the epicotyl. There is a four-strand system at the cotyledonary node, since the epicotylary strands become attached to late-formed secondary xylem just above the cotyledonary node.

#### SUMMARY AND DISCUSSION

Since his survey of the foliar nodal anatomy of dicotyledons (Sinnott, 1914), a fourth type of nodal arrangement, previously known in cotyledonary nodes (Thomas, 1907) but not considered by Sinnott, has recently



been demonstrated to occur at the foliar nodes of a number of dicotyledons (Bailey and Swamy, 1950; Money, Bailey and Swamy, 1949; Swamy, 1953).

The three types of foliar nodal anatomy recognized by Sinnott are as follows:

(a) The *trilacunar* condition, in which three bundles supply the leaf, each causing a gap of its own in the primary vascular cylinder.

(b) The *unilacunar* condition, where one or three leaf traces depart through a single gap in the primary stele.

(c) The *multilacunar* condition where more than three bundles are related to a corresponding number of independent gaps in the primary stele.

Sinnott regarded the trilacunar nodal condition as a very ancient type in the angiosperms, since it occurs in a great majority of the Archichlamydeae. He thought that the unilacunar form was derived from this in some families (1) by the reduction and elimination of the two lateral strands, and in other families (2) by the approximation of the median and lateral strands forming an aggregation of three strands related to a single gap in the stele. The multilacunar form he thought to have arisen by amplification of the number of independently attached lateral strands.

Further, in their series of investigations of the phylogeny of angiosperms, Sinnott and Bailey (1914) regarded the primitive angiosperm leaf as a simple one with palmate venation, possibly stipulate, and provided with three main bundles arising separately at the node. Leaves with parallel venation and those with sheathing leaf bases were observed to be associated with the multilacunar type of node, whereas exstipulate leaves usually exhibited a unilacunar nodal condition. Both of these observations tended to substantiate Sinnott's theory of the derivation of other nodal types by amplification and reduction.

Many dicotyledonous families are predominantly tri-, uni-, or multilacunar but in some families much variation occurs and transitions have been recorded among these three types. The fact that a fourth type of foliar nodal anatomy is now known to occur in the Austrobaileyaceae (Bailey and Swamy, 1949), Monimiaceae (Money, Bailey and Swamy, 1950), and Chloranthaceae (Swamy and Bailey, 1950; Swamy, 1953 a and b), coupled with the common occurrence of such a type of structure in cotyledonary nodes makes it essential to determine whether all types of unilacunar nodes are derived from trilacunar ones since the possibility exists that the fourth type of nodal anatomy may actually be a primitive rather than a reduced one. This fourth type of structure exhibits a single gap through which two discrete strands supply the leaf base, a condition that characterizes many of the gymnosperms and ferns.

The trilacunar arrangement was considered the more primitive condition in the angiosperms since it occurred most frequently in the Ranales and Rosales, which have been regarded as similar to the ancestral angiosperms in other anatomical features. Since the greater number of angio-

sperm families are trilacunar, and since the other nodal forms were thought to be modifications of this by reduction and amplification, its primitiveness has not been questioned until the unilacunar double-trace condition was demonstrated in several ranalian families.

There appears to be insufficient evidence to support the theory that the unilacunar condition is derived in all cases by reduction, especially when nodal arrangements in the vascular plants as a whole are considered. Examination of the transitional forms indicates that the double-trace unilacunar form may be the most primitive arrangement in the angiosperms.

If the unilacunar nodal condition was thought to be derived in some cases by the fusion, or by the loss, of one pair of lateral traces and gaps, could not the single trace of the unilacunar form also have arisen from the fusion of two (unilacunar) traces or by the loss of one trace? In this case, could the primitive number of foliar strands be even rather than odd?

It has been well established that within the woody Ranales primitive morphology of a given plant part is usually accompanied by specialization of other structures, so that no one taxonomic group is conspicuously the most primitive. The primitive characters seem to be divided among a diverse group of families. Therefore, it is not possible to establish which type of nodal anatomy is primitive by correlation with other primitive features; moreover, all four types of nodal anatomy occur in this group. This situation renders dubious Sinnott's correlative argument for the primitiveness of the trilacunar node, and suggests that valid comparative evidence for the primitive nodal condition in angiosperms must consider the Pteropsida as a whole, living and fossil, in an attempt to distinguish the basic nodal pattern in the complex out of which the angiosperms seem to have arisen.

It appears that among the ferns, Cycadofilices, Cordaitales, Bennettitales, Coniferales, Ginkgoales and *Ephedra*, the foliar strand, although often much divided in the petiole and lamina, departs from the primary body of the stele through a single gap. In these groups, the foliar bundles seem often to be *double* in nature.

In most of the Osmundaceae (Tansley, 1907; Scott, 1923; Sinnott, 1911) there is a single foliar strand departing from a single gap in the primary stele. In *Osmunda javanica* Blume (Posthumus, 1924), there is a double leaf trace, each strand with a distinct protoxylem group. The Gleicheniaceae and Ophioglossaceae possess a single gap with one trace, although young stages frequently exhibit a double trace in their first leaves (Bower, 1899, 1908). In all the members of the Marattiaceae, even in young plants of *Angiopteris* though not in the older plants, the condition at the base of the petiole is a leaf trace consisting of *two bundles*, each with a distinct protoxylem group, which depart through a single gap in the stele (Sinnott, 1911). In the fossil ferns of the Carboniferous, *Psaronius* and members of the Botryopteridae, Scott (1900) reports two distinct foliar traces.

Potonié (1896) and Scott (1900) have recorded that most of the Cycadofilices have two distinct foliar traces although fusion of these frequently occurs in the petiole. Sections of the fossil stems of *Lyginodendron* Old-

*hamium*, *Calamopitys Saturni* and *Medullosa anglica* show two distinct traces passing through the cortex to the base of each petiole, with fusion of these two strands occurring at various levels in the petiole.

The adult plants of the living Cycads exhibit an extremely complex vasculature of the petiole and in some cases the nodal structure is confused by numerous pairs of lateral traces, each of which causes a gap of its own in the stele.

In the Cordaitales, *Mesoxylon* (Traverse, 1950), *Poroxylon* and *Cordaites* (Williamson, 1898) all possessed a double leaf trace departing through a single gap in the stele, which seems to have been typical of the group as a whole. In the Bennettitales, although the vascular supply to the adult leaves is much more simple than in the living and fossil Cycads, the beautifully preserved embryos exhibit the double nature of the vascular strand, and at the cotyledonary node two distinct vascular strands supply each cotyledon, dividing in the tissues of the leaf to form as many as six traces to each embryo leaf (Wieland, 1916). In *Williamsoniella*, however, there is a double trace in adult leaves also (Thomas, 1915).

Jeffrey (1905) indicated the prevalence of a double foliar trace in the Coniferales. In the Abietineae the central strand in the leaf is nearly always double in origin, and this is particularly marked in the early leaves. The two traces are clearly evident in *Araucaria*.

In many of these groups possessing a double foliar strand, for example *Mesoxylon*, *Poroxylon*, *Cordaites*, the Bennettitales and the Coniferales, it has been assumed that these leaf bundles arise from the same main vascular strand (Florin, 1931). These, then, exhibit the continual dichotomy of an initial main strand and uphold the "telome theory" (Zimmerman, 1930). However, in the Ginkgoales and Gnetales, and in several members of the Angiospermae which will be considered later, the two strands of the leaf depart through a single gap in the stele, and each of these is connected to a separate bundle of the eustele.

*Ginkgo biloba* is reported as having two distinct foliar traces in both long and short shoots (Gunckel and Wetmore, 1946a and b), and Thomas (1907) has observed a similar structure in the cotyledons. The base of the cotyledon is provided with a double bundle and the halves of this separate widely as they pass through the tissues of the embryonic leaves. Gunckel and Wetmore figure the vasculature of the stem and leaf systems emphasizing the connection of each strand of this double bundle with an entirely different and independent bundle of the eustele.

In the seedlings and young adult plants of *Ephedra andina* (Steeves, unpublished) two distinct foliar traces depart from the primary body of the stele through a unilacunar gap (as was also shown earlier in this thesis). These again arise from two entirely independent bundles of the eustele. Sinnott (1914) emphasized that in species of *Ephedra* two distinct gaps occur, but these are gaps in the secondary and not the primary body. This arrangement can therefore be discounted since it is of secondary modification. A similar condition occurs in *Trimenia* and occasionally in *Agathis*. The nodal condition in other members of the Gnetales is ex-



tremely complex in the adult forms, but in the seedlings of *Welwitschia mirabilis* (Rodin, 1953) the cotyledons show two longitudinal vascular bundles entering at the base in cleared seedlings, each dichotomises as it enters the tissue of the leaf and the two lateral bundles of these divide again.

In *Agathis* of the Araucariaceae, a condition similar to that observed in some *Ephedras* has been recorded by Thomson (1913) and the primary arrangement of two distinct vascular strands to the leaves is confused by the insertion of a small segment of secondary wood between the two bundles, causing what appear to be two separate strands in the stele.

This survey of Pteropsida exclusive of the angiosperms can be summarized as follows:

- (1) Almost all of these groups exhibit a unilacunar nodal condition.
- (2) Although frequently there is a single leaf trace, in the majority of the groups examined, two distinct foliar traces depart through the single gap in the primary stele.
- (3) In those cases where a complex condition has been observed in the older plant, the primary condition in the young plants or at the cotyledonary node in the seedling is almost always a double vascular supply to each young leaf or cotyledon from a single gap in the stele.
- (4) Occasionally two gaps occur in the secondary body, but the primary condition in these cases is a single gap with two foliar traces.

This prevalence of the unilacunar, double-trace condition in lower Pteropsida suggests that this nodal arrangement, rather than a trilacunar one, may have been the primitive nodal condition in ancestral angiosperms.

Since the nodal arrangements which occur more frequently in the angiosperms exhibit odd numbers of traces to the leaf base, the question arises as to how these one, three, five, etc. traces could have been derived from the two-trace condition. Since fusion occurs frequently between the two foliar traces of the angiosperms and lower Pteridophyta which possess the fourth type of nodal anatomy, it seems possible that in those cases where a single leaf trace supplies the petiole from a unilacunar gap, this trace may actually represent a fusion bundle.

In *Clerodendron*, *Austrobaileya*, *Trimenia* and *Ascarina* the two foliar traces may unite at varying levels in the petiole or lamina to form a single vein. In *Amborella trichopoda* (Bailey and Swamy, 1948) a single strand appears to depart from a unilacunar gap in the stele, but at sub-nodal levels this strand is seen to consist of two distinct parts which arise from independent portions of the stele (Bailey, unpublished). The fusion of foliar traces observed in the petiole or lamina of the plants cited above has been carried to sub-nodal levels in *Amborella* giving rise to a single trace by the fusion of two initial traces.

*Ascarina* and *Hedyosmum* of the Chloranthaceae (Bailey and Swamy, 1949; Swamy 1935a,b,c) possess two distinct strands related to a single gap in the stele. In *Hedyosmum* the two strands bifurcate and the two median strands of these then fuse to form a single median strand, while

the two lateral strands bifurcate again, producing a total of five strands. In *Chloranthus* and *Sarcandra*, two vascular strands depart from a unilacunar gap and these immediately bifurcate; the two median members fuse, forming three vascular strands, which become the mid-rib bundles of the leaf. Two smaller subsidiary veins vascularize the marginal portions of the leaf (cf. below).

In the Monimiaceae (Money, Bailey and Swamy, 1950), the family as a whole is uniformly unilacunar. The leaves of *Trimenia* are vascularized by two discrete strands which frequently remain separate throughout the entire petiole and costa of the lamina, each strand supplying by its subdivisions one half of the bilateral leaf, as in *Clerodendron trichotomum*. In some cases, in the leaves of *Trimenia* these two strands may merge to form a single midvein, particularly in the middle and upper portions of the leaf. In all cases the two independent strands arise from two distinctly separate portions of the eustele. In *Piptocalyx* there are two foliar strands which depart from the unilacunar gap, and which bifurcate to produce four strands. The two median strands of this group of four may fuse in the petiole to produce three strands, and in the lamina these coalesce, forming a single midvein. In other words, by a process of bifurcation and fusion, the number of strands has gone from an even number, 2 and 4, to an odd number, first 3 and then 1.

In *Hortonia angustifolia*, *Anthobembix Brassii* and *Mollinedia Rusbyana* (Money, Bailey and Swamy, 1950) (Monimiaceae) increasing odd numbers of foliar traces depart from the unilacunar gap at the node. The number of foliar traces is three in *Hortonia*, five in *Anthobembix* and seven in *Mollinedia*. In each case these arose initially from two distinct strands of the eustele, and this can be demonstrated by following the origin of the foliar traces through several nodes and internodes below.

From the examples cited above, it therefore appears certain that an odd number of foliar traces can arise by the division and fusion of an even number of strands. Particularly, it seems likely that the odd number (1 or 3) of traces related to the median gap of so many angiosperms could have been derived originally from the two-trace condition.

However, the cases of multiple-strand formation mentioned above are not examples of the formation of tri- or multilacunar from unilacunar nodes, because the odd number of strands departs from a single gap as did the primitive pair of traces. Can such multiple traces come to occupy separate gaps? Or is there evidence for the evolutionary addition of lateral traces with new gaps? Acceptance of the hypothesis that the unilacunar node is primitive requires that at least one of these possibilities be demonstrable.

It has been generally accepted since Sinnott's work that the multilacunar condition is specialized, and has been derived from the trilacunar by the addition of laterals with new gaps. It would seem possible for the unilacunar to give rise to the trilacunar in the same fashion. In other words, there is no particular reason to suppose that the kind of amplifica-

tion which resulted in the multilacunar node could not also produce the trilacunar node from the unilacunar one.

The addition of laterals in different gaps to a unilacunar system is adequately shown in the series of nodal forms of Chloranthaceae described by Bailey and Swamy. The primitive form here is undoubtedly the two-trace unilacunar type, as discussed above. However, in *Chloranthus* and *Sarcandra*, where the two traces branch and fuse to form three, as mentioned, two "subsidiary" traces which depart from gaps at right angles to the main gap also vascularize each leaf. The gaps in the eustele in which these traces arise are present but unoccupied in the less specialized Chloranthaceae.

It was mentioned above that in *Agathis* and some species of *Ephedra* a two-trace unilacunar condition becomes converted into an apparent "bilacunar" one by development of a wedge of secondary tissue in the gap parenchyma of the stele, between the two traces (Sinnott, 1914). It seems possible that multiple traces in one gap such as were described above for the Chloranthaceae and Monimiaceae could become separated in a similar way and, by extension of this phenomenon precociously to the primary body, come to occupy separate gaps. A tri- or multilacunar condition would thus have evolved.

It is of great interest that a double trace has been recorded in the cotyledons of so many angiosperms (Thomas, 1907) which have an odd number of traces in adult leaves. In the lower Pteropsida also, the double-trace condition is found in the cotyledons in many cases where a more complex and apparently specialized pattern appears at later nodes. On the other hand, among the plants whose mature nodes are unilacunar with two traces, no examples have been found in which the cotyledonary node does not exhibit similar structure (few, however, have been studied). It is tempting to consider that this cotyledonary condition represents the persistence of a primitive morphology. In cotyledons of *Clerodendron trichotomum*, which have been carefully studied with this question in mind, there occurs sporadically a median protoxylem strand which has arisen as an upward extension of a protoxylem pole of the young root and is apparently not a part of the intrinsic vascular pattern of the cotyledons. It seems likely that other cases where three cotyledonary strands have been observed may be instances of a similar complication.

However, seedlings of many dicotyledons (according to an unpublished survey by one of us) have an odd number of cotyledonary traces from a single gap, which are divided from two strands by branching and fusion in a manner similar to that described above for mature nodes of certain Monimiaceae. A common condition (in seedlings) is for the two original traces to branch once and the two median branches to fuse; giving a total of three traces in the petiole. This is found, for example, in Rosaceae, Leguminosae, *Hamamelis* and *Betula*. In others, e.g. *Impatiens* and *Acer*, a greater odd number of strands is produced by further branching. Laterals occupying separate gaps are present in Magnoliaceae and *Degeneria*, though the main gap shows a two-trace condition (Swamy, 1949). The tendency of the unilacunar pair of traces to fuse in the cotyledon, as ob-



served in *Amaranthus* and *Anchusa*, seems to be carried further to form a single unilacunar trace in the Cruciferae, Primulaceae, and *Celastrus scandens*. A pair of distinct parallel traces such as are found in *Clerodendron trichotomum* occurs commonly in Solanaceae and Labiatae.

The median bundle in the uni-, tri- and multilacunar types requires closer investigation. The whole question as to the exact nature of this bundle could be ontogenetic. Does the median bundle represent (a) two distinct procambial strands which have merged during differentiation; (b) two procambial strands, only one of which has differentiated, or (c) only a single procambial strand? And in those cases where there are two distinct foliar strands, are these developed from (a) two distinct procambial strands which have undergone normal differentiation, or (b) the lateral portions of one procambial strand, separated by a median layer which has failed to differentiate into vascular tissue?

In *Clerodendron trichotomum*, all the different leaf forms (excluding the floral appendages) are supplied in a similar manner, viz. by two discrete vascular strands from a single gap. In each case these two foliar traces arise separately from independent bundles of the eustele. In the foliage leaves, bud scales, floral bracts, and cotyledons these two traces originate from two distinct procambial strands. These represent, therefore, two separate procambial strands which have undergone normal differentiation. Similarly, in *Austrobaileya*, where each leaf is supplied by two discrete vascular traces arising from two independent portions of the eustele (Bailey and Swamy, 1949), these foliar traces have differentiated normally from two separate procambial strands. The two separate foliar traces of *Triplaris* (Money et al., 1950) also arise by the normal differentiation of two procambial strands. To the extent that this kind of evidence can indicate the nature of the foliar traces, the present observations suggest that the two leaf traces in the forms studied are distinct, and not the result of abnormal differentiation of a single strand.

This fourth type of nodal anatomy exhibited by *Clerodendron trichotomum*, which occurs in a great many dicotyledonous seedlings at the cotyledonary node, and in the adult plants of several ranalian genera, is a type of nodal structure which must be considered of phylogenetic importance. The double-trace, unilacunar condition does not conform with Sinnott's unilacunar form since it is not attained by modifications of a trilacunar node. The present survey of nodal anatomy, and the ontogenetic studies on *Clerodendron trichotomum* presented here, indicate that the fourth type of nodal structure may ultimately prove to be the nodal arrangement of ancestral angiosperms. In order that such a theory could become a working hypothesis upon which phylogenetic investigations could be based, further extensive ontogenetic studies are needed. It is tentatively suggested here that the unilacunar double-trace condition was the primitive structure of the node among the Tracheophyta, and that the three nodal forms described by Sinnott for the angiosperms are specializations of this. Accordingly, Sinnott's hypothesis of nodal evolution in dicotyledons can be modified as follows (Fig. 17): (a) The two-trace unilacunar condition

can give rise to a single trace by fusion; (b) the double-trace unilacunar condition can give rise to the trilacunar condition by fusion and the addition of one pair of lateral traces and gaps. The trilacunar form can give rise to a unilacunar condition, as it appears frequently to have done, by the loss of laterals, and to a multilacunar form by the addition of pairs of laterals as Sinnott has already postulated.

In conclusion, it should be emphasized that excessive attention has been focused in the past upon the addition or elimination of pairs of independently attached laterals, and to topographical features at the nodal level. Greater consideration should be given in the future to detailed investigations of vascular tissues related to the median gap, and to tracing these structures both downwards in the stem and outwards into the petiole and lamina of the leaf. Bifurcations and fusions of vascular strands, and transitions from an *even* to an *odd* number of such strands, occur at various levels

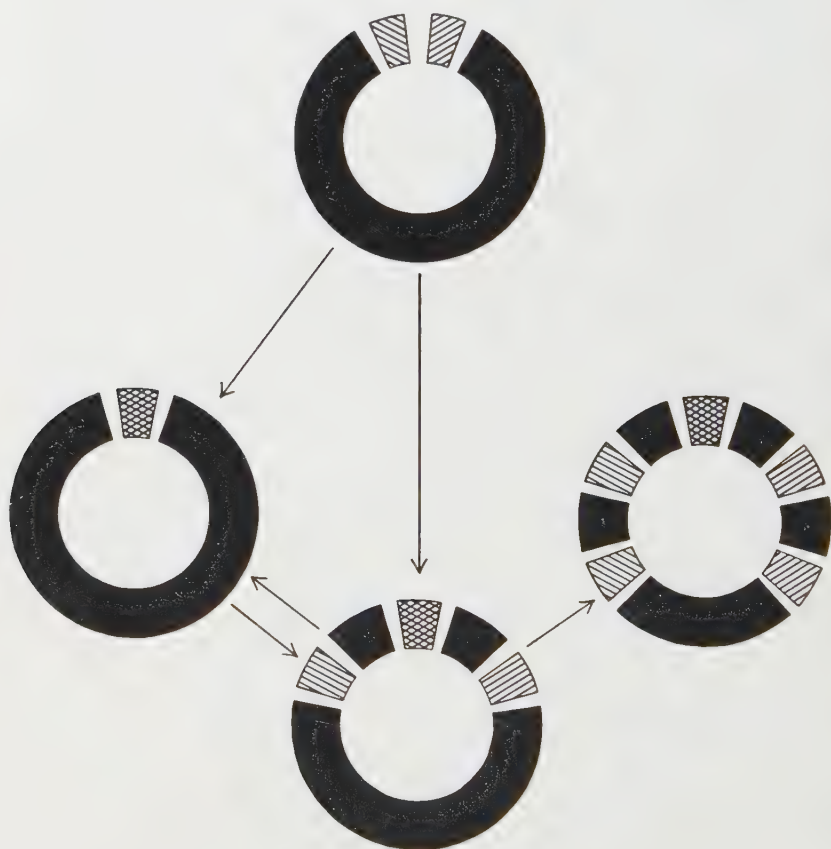


FIGURE 17

THE POSSIBLE DERIVATION OF THE DICOTYLEDONOUS NODAL FORMS FROM THE UNILACUNAR DOUBLE TRACE CONDITION.

of the stem and leaf. Structures which appear to be similar at the nodal level may not be truly homologous, and conversely differences which seem outstanding at the nodal level may acquire a different significance where comprehensive developmental studies at successive levels of the stem and leaf are made.

#### LITERATURE CITED

- ASKENASY, E. 1880. Ueber eine neue Methode, um die Vertheilung der Wockstumsintensität in wachsenden Theilen zu bestimmen. Verhand. Naturhis.-medizin: Ver. zu Heidelberg 2: 7-153.
- AVERY, G. S., JR. 1933. Structure and development of the tobacco leaf. Amer. Jour. Bot. 20: 565-592.
- BAILEY, I. W. AND C. G. NAST. 1943. The comparative morphology of the Winteraceae. II. Carpels. Jour. Arnold Arb. 24: 472-481.
- BAILEY, I. W. AND B. G. L. SWAMY. 1948. *Amborella trichopoda* Baill., a new morphological type of vesselless dicotyledon. Jour. Arnold Arb. 29: 245-254.
- . 1949. The morphology and relationships of *Austrobaileya*. Jour. Arnold Arb. 30: 211-226.
- BOKE, N. H. 1940. Histogenesis and morphology of the phyllode in certain species of *Acacia*. Amer. Jour. Bot. 27: 73-90.
- BOWER, F. O. 1899. Studies on the morphology of spore producing members. Part 4. The Leptosporangiate ferns. Phil. Trans. Roy. Soc. 192b: 29-138.
- . 1908. Origin of a land flora. Macmillan and Co., Ltd. London.
- CHAUVEAUD, G. 1911. L'appareil conducteur des plantes vasculaires et les phases principales de son évolution. Ann. des Sci. Nat., Bot. Ser. 9. 13: 113-438.
- . 1921. La constitution des plantes vasculaires révélée par leur ontogénie. 3rd Ed. Payot et Cie, Paris.
- COMPTON, R. H. 1912. An investigation of the seedling structure in the Leguminosae. Linn. Soc. London, Jour. Bot. 41: 1-132.
- DANGEARD, P. A. 1889. Recherches sur la mode d'union de la tige et de la racine chez les Dicotylédones. Botaniste Ser. 1. 1: 75-125.
- . 1913. Observations sur la structure des plantules chez les Phanérogames dans rapports avec l'évolution vasculaire. Soc. Bot. de France Bul. 60: 73-80, 113-120.
- DEBENHAM, E. M. 1939. A modified technique for the microscopic examination of xylem of whole plants or plant organs. Ann. Bot. 3: 369-373.
- DE TOMASI, J. A. 1936. Improving the technique of the Feulgen stain. Stain Technology. 11: 137-144.
- EAMES, A. J. 1931. The vascular anatomy of the flower with refutation of carpel polymorphism. Ann. Bot. 18: 147-188.
- AND L. H. MACDANIELS. 1947. An introduction to plant anatomy. 2nd Ed. New York, McGraw-Hill Book Co.
- ESAU, K. 1942. Vascular differentiation in the vegetative shoot of *Linum*. I. The procambium. Amer. Jour. Bot. 29: 738-747.
- . 1943a. Vascular differentiation in the vegetative shoot of *Linum*. II. The first phloem and xylem. Hilgardia. 30: 248-255.
- . 1943b. Origin and development of primary vascular tissues in seed plants. Bot. Rev. 9: 125-206.
- . 1945. Vascularization of the vegetative shoot of *Helianthus* and *Sam-bucus*. Amer. Jour. Bot. 32: 18-29.

- ESAU, K. 1953. Plant anatomy. John Wiley and Sons, Inc. New York.
- . 1954. Primary vascular differentiation in plants. *Bot. Rev.* 29: 46–86.
- FLORIN, R. 1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. *Svenska Vetensk. Acad. Handl. Ser. 5.* 10: 1–588.
- FOSTER, A. S. 1929. Investigations on the morphology and comparative history of development of foliar organs. I. The foliage leaves and cataphyllary structures in the horsechestnut (*Aesculus Hippocastanum* L.), cont'd. *Amer. Jour. Bot.* 16: 475–501.
- . 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. *Stain Technology* 9: 91–92.
- . 1935. A histogenetic study of the foliar determination in *Carya Buckleyi* var. *arkansana*. *Amer. Jour. Bot.* 22: 88–147.
- . 1936. Leaf differentiation in angiosperms. *Bot. Rev.* 2: 349–372.
- GARRISON, R. 1949a. Origin and development of axillary buds: *Syringa vulgaris* L. *Amer. Jour. Bot.* 36: 205–213.
- . 1949b. Origin and development of axillary buds: *Betula papyrifera* Marsh. and *Euptelea polyandra* Sieb. et Zucc. *Amer. Jour. Bot.* 36: 379–389.
- GREGOIRE, V. 1938. La morphogénèse et l'autonomie morphologique de l'appareil floral. I. La carpelle. *Cellule.* 47: 287–452.
- GUNCKEL, J. E. AND R. H. WETMORE. 1946a. Studies on the development of long and short shoots of *Ginkgo biloba* L. I. The origin and pattern of development of the cortex, pith and procambium. *Amer. Jour. Bot.* 33: 285–295.
- . 1946b. Studies on the development of long and short shoots of *Ginkgo biloba* L. II. Phyllotaxis and the organization of the primary vascular system; primary phloem and primary xylem. *Amer. Jour. Bot.* 33: 532–543.
- HILL, T. G. AND E. DE FRAINE. 1913. A consideration of the facts relating to the structure of seedlings. *Ann. Bot.* 27: 257–272.
- JEFFREY, E. C. 1905. Comparative anatomy and phylogeny of the Coniferales. Part 2. Abietineae. *Memoirs Boston Soc. Nat. Hist.* 6: 1–37.
- . 1917. The anatomy of woody plants. Chicago, University of Chicago Press.
- JOHANSEN, D. A. 1940. Plant Microtechnique. McGraw-Hill Book Company, New York.
- KAPLAN, R. 1937. Über die Bildung der stele aus dem Urmeristem von Pteridophyten und Spermatophyten. *Planta.* 27: 224–268.
- KUMAR, L. S., A. ABRAHAM AND S. SOLOMON. 1942. A technique for the anatomical study of root parasitism. *Ann. Bot.* 6: 177–182.
- LAM, H. J. 1919. The Verbenaceae of the Malayan Archipelago. M. de Waal, Groningen. 273–275.
- LEHMBERG, K. 1923–24. Zur Kenntnis des Baues und der Entwicklung der wasserleitenden Bahnen bei der Sonnenblume (*Helianthus annuus*). Beihefte. Botanischen Centralblatt. 40: 183–236.
- LENOIR, M. 1920. Évolution du tissu vasculaire chez quelques plantules des dicotylédones. *Ann. des Sci. Nat., Bot. ser. 10,* 2: 1–123.
- LUBBOCK, J. 1892. A contribution to our knowledge of seedlings. Paul, Trench, Truber and Co. 372–374.
- MILLER, H. A. AND R. H. WETMORE. 1946. Studies on the developmental anatomy of *Phlox drummondii*. Hook. III. The apices of the mature plant. *Amer. Jour. Bot.* 33: 1–10.

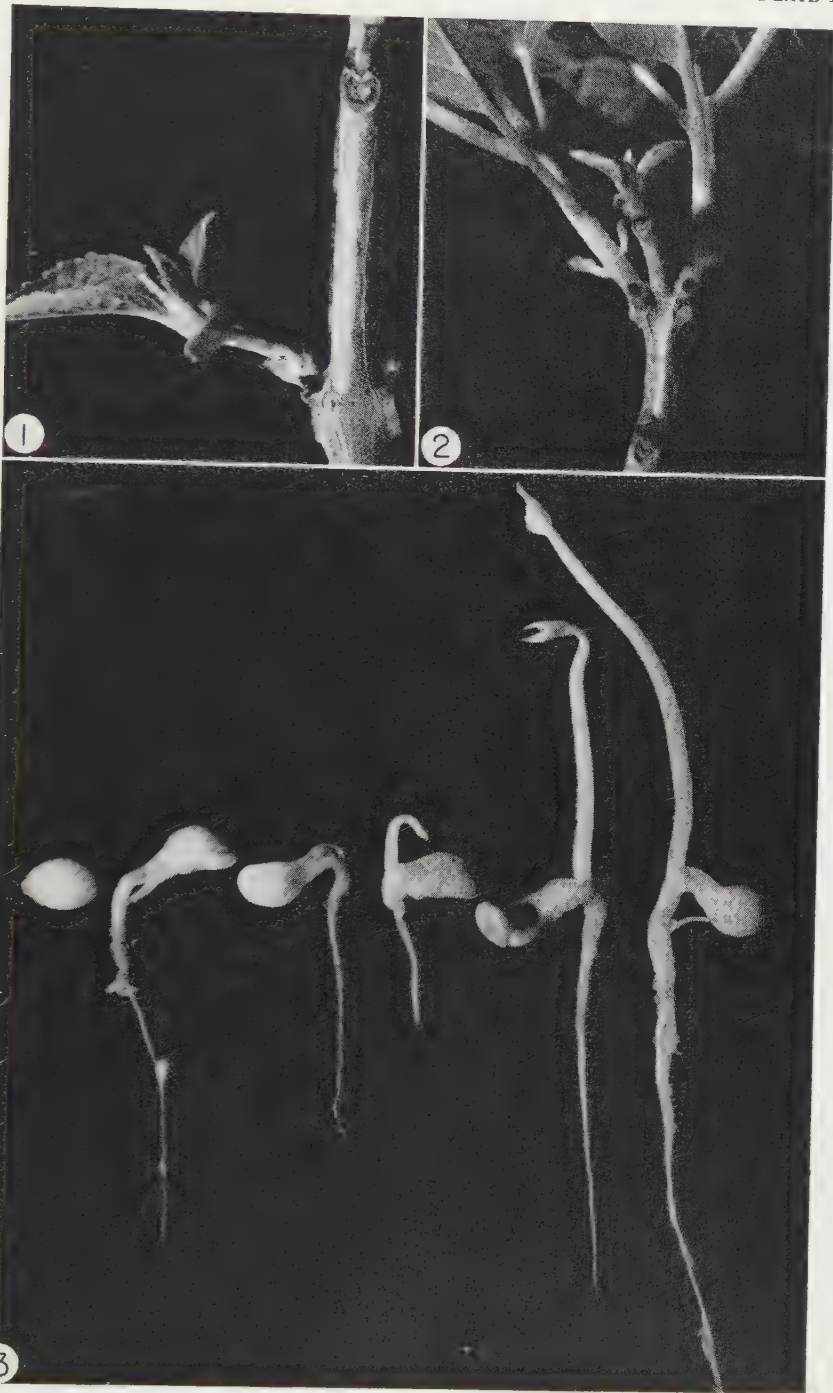


- MONEY, L. L., I. W. BAILEY AND B. G. L. SWAMY. 1950. The morphology and relationships of the Monimiaceae. Jour. Arnold Arb. 31: 372-404.
- MULLER, C. 1937. La tige feuillée et les cotylédons des Viciées à germination hypogée. Cellule. 46: 195-354.
- POSTHUMUS, O. 1924. On some principles of stelar morphology. Extrait du Recueil des Travaux Botaniques Néerlandais. 21: 111-296.
- POTONIÉ, H. 1896. Die floristische Gliederung des deutschen Carbon und Perm. Jahrb. preuss. geol. Landesanst. Heft 21.
- PRATT, C. AND R. H. WETMORE. 1951. A paraffin method for refractory plant materials. Stain Technology. 26: 251-253.
- RODIN, R. J. 1953. Seedling morphology of Welwitschia. Amer. Jour. Bot. 40: 371-378.
- SARGANT, E. 1900. A new type of transition from stem to root in the vascular system of seedlings. Ann. Bot. 14: 633-638.
- SCHMIDT, A. 1924. Histologische Studien an phanerogamen Vegetationspunkten. Bot. Arch. 8: 345-404.
- SCOTT, D. H. 1900. Studies in fossil botany. A. and C. Black, London.
- . 1923. Studies in fossil botany. Volume 2. 3rd Ed. A. and C. Black, London.
- SINNOTT, E. W. 1911. Evolution of the Filicinean leaf-trace. Ann. Bot. 25: 167-192.
- . 1914. Investigations on the phylogeny of the angiosperms. I. The anatomy of the node as an aid in the classification of angiosperms. Amer. Jour. Bot. 1: 303-322.
- AND I. W. BAILEY. 1914. Investigations on the phylogeny of the angiosperms. III. Nodal anatomy and the morphology of stipules. Amer. Jour. Bot. 1: 441-453.
- . 1915. Investigations on the phylogeny of the angiosperms. V. Foliar evidence as to the ancestry and early climatic environment of the angiosperms. Amer. Jour. Bot. 2: 1-22.
- SMITH, G. F. AND H. KERSTEN. 1942. The relation between xylem thickenings in the primary root of *Vicia faba* seedlings and elongation, as shown by soft x-ray irradiation. Bull. Tor. Bot. Club. 69: 221-223.
- STERLING, C. 1945. Growth and vascular development in the shoot apex of *Sequoia sempervirens* (Lamb.) Endl. II. Vascular development in relation to phyllotaxis. Amer. Jour. Bot. 32: 380-386.
- . 1947. Organization of the shoot of *Pseudotsuga taxifolia* (Lamb.) Britt. II. Vascularization. Amer. Jour. Bot. 34: 272-280.
- SWAMY, B. G. L. 1949. Further contributions to the morphology of the Degeneriaceae. Jour. Arnold Arb. 30: 10-38.
- . 1953a. The morphology and relationships of the Chloranthaceae. Jour. Arnold Arb. 34: 375-408.
- . 1953b. *Sarcandra Irvingbaileyi*, a new species of vesselless dicotyledon from South India. Proc. Nat. Ins. Sci. India. 19: 301-306.
- . 1953c. A taxonomic revision of the genus *Ascarina* Forest. Proc. Nat. Inst. Sci. India. 19: 371-388.
- AND I. W. BAILEY. 1950. *Sarcandra*, a vesselless genus of the Chloranthaceae. Jour. Arnold Arb. 31: 117-129.
- TANSLEY, A. G. 1907. Lectures on the evolution of the Filicinean vascular system. VIII. Osmundaceae and Ophioglossales. New Phyt. 6: 253-269.
- THODAY, D. 1939. The interpretation of plant structure. Nature. 144: 571-575.

- THOMAS, E. N. 1907. A theory of the double leaf trace founded on seedling structure. *New Phyt.* **6**: 77-91.
- . 1914. Seedling anatomy of the Ranales, Rhoadales, and Rosales. *Ann. Bot.* **28**: 695-733.
- THOMAS, H. H. 1915. On *Williamsoniella*, a new type of Bennettitid flower. *Phil. Trans. Roy. Soc.* **207**: 113-148.
- THOMSON, R. B. 1913. On the comparative anatomy and affinities of the Araucarineae. *Phil. Trans. Roy. Soc.* **B204**: 1-50.
- TRAVERSE, A. 1950. The primary vascular body of *Mesoxylon Thompsonii*, a new American Cordaitalean. *Amer. Jour. Bot.* **37**: 318-325.
- VAN TIEGHEM, P. 1891. *Traité de botanique*. 2nd Ed. Paris. Librairie F. Savy.
- WARDLAW, C. W. 1943. Experimental and analytical studies of Pteridophytes. I. Preliminary observations on the development of buds on the rhizome of the Ostrich Fern (*Matteuccia struthiopteris* Tod.). *Ann. Bot.* **7**: 171-184.
- WIELAND, G. R. 1916. American fossil Cycads. Vol. 11. 142.
- WILLIAMSON, W. C. 1898. Organization of fossil plants of coal measures. Part xii. *Phil. Trans.* 407.
- ZIMMERMAN, W. 1930. *Die Phylogenie der Pflanzen*. Jena.

## PLATE I

1 and 2, expanding terminal and axillary buds of *Clerodendron trichotomum*, showing the cataphylls and transition leaves. Note the retarded growth of the terminal bud (2).  $\times 2.5$ . 3. Early stages in the germination of the seed of *C. trichotomum*, from left to right of the photograph: (a) Seed with testa removed. (b) Elongation of radicle. (c) Emergence of epicotyl. (d) Beginning of elongation of crook-shaped epicotyl. (e) and (f) Elongation and straightening of epicotyl.  $\times 2$ .



MARSDEN AND BAILEY, CLERODENDRON TRICHOTOMUM

## A MONOGRAPH OF THE GENUS PHILADELPHUS \*

SHIU-YING HU

Subgenus II. *Euphiladelphus*, subg. nov.*Philadelphus* subg. II. *Euphiladelphus*, subg. nov.*Philadelphus* Reihe. 1. *Corticatae* Koehne, Deutsche Dendr. 179, 180. 1893.*Philadelphus* Reihe 3. *Decorticatae racemoseae* Koehne, l. c. 180, 182.*Philadelphus* Reihe 4. *Decorticatae pauciflorae* Koehne, l. c. 180, 184, pro parte.*Philadelphus* Sect. 2. *Stenostigma* Koehne in Gartenfl. 45: 450. 1896, pro parte; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77, 81. 1904, pro parte.TYPE SPECIES: *P. coronarius* Linn.

Frutex erectus, inflorescentiis racemosis, vel floribus ternatis vel solitariis, hypanthiis obconicis, subcampanulatis vel subglobosis, glabris vel pubescentibus; staminibus 25 usque ad 90; ovariis semi-inferioribus vel inferioribus; stylis partibus superis plerumque liberis, stigmatibus linearibus vel dilatis; capsulis ellipsoideis vel subglobosis; seminibus longi- vel brevi-caudatis; foliis oppositis, ovatis, serratis, denticulatis vel integris, triplinerviis or quintuplinerviis, gemmis axillaribus inclusis.

This subgenus has a wide range of distribution in the northern temperate zone, between latitudes 25°–50° N. From southern Europe eastward, across the mainland of Asia to Japan and then from western North America to south eastern United States its range is almost continuous. The only two interruptions occur in western and central Asia and the central and northern sections of the Great Plain States in the United States. Obviously the primary cause of these disjunctions is low precipitation. The Amur River region in northeastern Asia and the Columbia River region in western North America register its highest latitudinal distribution and the Himalayan region in Asia and the Rocky Mountain region in North America mark its highest altitudinal distribution. It has 41 species in three sections. Their distributions are as illustrated in Maps 2 and 3.

Section 3 *Pauciflorus* (Koehne), stat. nov.*Philadelphus* subg. II. *Euphiladelphus* sect. 3. *Pauciflorus* (Koehne), stat. nov.*Philadelphus* Reihe 4. *Decorticatae pauciflorae* Koehne in Deutsche Dendr. 180, 184. 1893, pro parte.

\* Continued from volume XXXV, page 333.



*Philadelphus* sect. *Poecilostigma* Koehne subsect. *Speciosi* Koehne in Gartenfl. 45: 450. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77, 79. 1904. — Engler, Pflanzenf. ed. 2. 18a: 193. 1930.

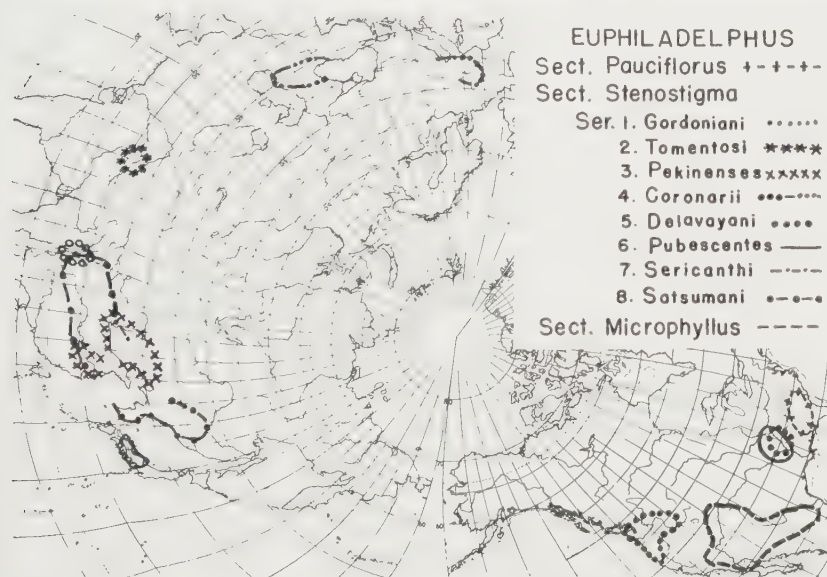
*Philadelphus* *Grandiflori* Rydb. in N. Am. Fl. 22: 163. 1905, in clavis, s. stat. — Beadle in Small, Man. South. Fl. 598. 1933.

*Philadelphus* ser. 4. *Speciosi* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.

TYPE SPECIES: *P. inodorus* Linn.

Arching shrub with slender branchlets sweeping the ground, the bark exfoliating; leaves ovate, ovate-elliptic, elliptic, or lanceolate, dentate, rarely subentire; flowers solitary, ternate or in true dichasia; sepals foliaceous, long acuminate; petals oblong or rhomboid, rounded or obtuse at the apex; stamens 60–90; ovary with highly attached placentas, the style equal or longer than the longest stamens, the apical end divided, the stigma oar-shaped, the adaxial surfaces longer than the abaxial ones; capsules ellipsoid or subobovoid, with median persistent sepals; seeds long-caudate. Two species, many varieties. Native of the southern Appalachian region of the United States.

The type species of this section, *P. inodorus* Linn., was discovered by Mark Catesby on the bank of the Savannah River between South Carolina and Georgia. Unfortunately his artist overlooked the critical leaf characters of the plant, and instead of the faintly denticulate triplinerved leaves he depicted entire pinnate-nerved leaves. Linnaeus validated the species on the basis of Catesby's description and illustration. In trying to present a contrasting character for distinguishing this American species



MAP 2. The distribution of the sections and series of the subgenus EUPHILADELPHUS.

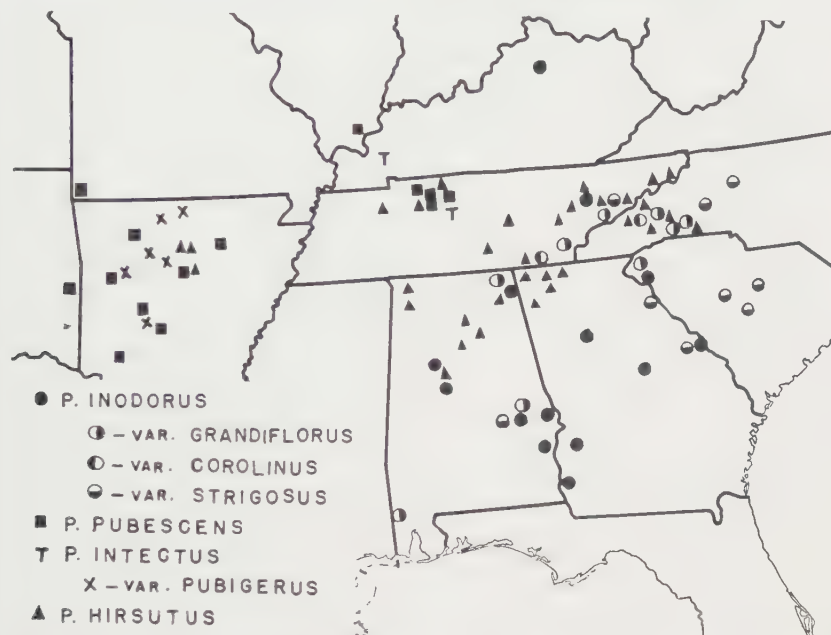
from the European one, he remarked "foliis integerrimis." Meanwhile, attempts at introducing this species from America to Europe were made. Dr. Dale in 1738 shipped both seeds and living plants to England. Miller who received this material failed to germinate the seeds. The living specimen that he planted in the Chelsea Garden was destroyed by the cold winter of 1740. There does not seem to be a successful introduction of the plant in Europe until the beginning of the nineteenth century. Thus from the time of the discovery of the first species of this section to the end of the eighteenth century the botanical records about *P. inodorus* Linn. were all from one source, that is, Catesby's Natural History of Carolina, and as a matter of fact the authors of these records, misled by the illustration, all stressed the entire leaf character of the plant. But among the natural population in this section of *Philadelphus* there is no plant that really possesses entire leaves. The leaves of some form may appear more nearly entire than the others, but leaves with small teeth actually exist on all variants, cultivated as well as the natural ones. By the beginning of the nineteenth century more plants were introduced from Carolina and Georgia to Europe under the name of *P. inodorus* Linn. As botanists were looking for an entire-leaved form to represent this binomial, the dentate-leaved material was named *P. grandiflorus* Willd. (1809), *P. laxus* Schrad. (1825), and half a dozen other synonyms as enumerated in Lavallée, Arb. Segrez. Enum. 114. 1877. The large amount of spontaneous material that I have examined convinces me that the formerly recognized species, *P. grandiflorus* Willd., and *P. laxus* Schrad., are merely different forms of a species with heterogeneous leaf shape, size and margins. Fostered by growers, propagated and distributed through cuttings, these forms have maintained their distinction in gardens since their discoveries. But when they are projected on the spectrum of variations exhibited by a large number of specimens collected from the homeland of *P. inodorus* Linn. they appear to be nothing but a few transitional forms. In this paper, these forms are treated as varieties.

Beadle in 1902 discovered a species with pubescent pedicels and hypanthia from the Coosa River region in Georgia. This discovery makes the second species of the section *Pauciflorus*.

This section is endemic to the southern Appalachian Mountains. The Great Smoky and the Lookout Mountains are the centers of the concentration of its species, and the Stamping Ground in Kentucky, Statesville in North Carolina, Santee River region in South Carolina, Coheelee Creek in Georgia and Mobile in Alabama mark the periphery of their overlapping ranges. The specimens collected from the cliffs on the Delaware River in Pennsylvania seem to be out of the range and they probably represent some escapes. As illustrated in Map 2, there seems to be no marked geographical separation between *P. inodorus* Linn. and *P. inodorus* Linn. var. *grandiflorus* (Willd.) Gray. *Philadelphus inodorus* Linn. var. *laxus* (Schrader) S. Y. Hu has been collected only once in nature, and that was on Great Smoky Mountain. *Philadelphus inodorus* Linn. var. *carolinus* S. Y. Hu occurs both in the Blue Ridge area of North Carolina and the

Lookout Mountains at the Georgia-Alabama-Tennessee border. *Philadelphus inodorus* Linn. var. *strigosus* Beadle is only known from the type locality and a plant cultivated in the Arnold Arboretum.

In this study, I have examined 191 specimens representing 161 collections that belong to this section, and have observed very little morphological modification which leads to speciation. This scarcity of variations apparently indicates the stability of the species of the sections.



MAP 3. The distribution of the major species of *Philadelphus* in southeastern United States.

#### KEY TO THE SPECIES

- A. Pedicels and hypanthia glabrous .....15. *P. inodorus*.  
 AA. Pedicels and hypanthia pubescent .....16. *P. floridus*.

15. *Philadelphus inodorus* Linn. Sp. Pl. 470. 1753. — Miller, Gard. Dict. [834]. 1768. — Walter, Fl. Carol. 146. 1788. — Willd. Sp. Pl. 2: 948. 1800. — Barton, Elem. Bot. pl. 18, fig. 1. 1803. — Michx. Fl. Bor. Am. 1: 283. 1803. — Aiton, Hort. Kew. ed. Alt., 3: 180. 1811. — Pursh, Fl. Am. Sept. 1: 329. 1814. — Elliott, Sketch 1: 538. 1821. — DC. Prodr. 3: 206. 1828. — Schrader in Linnaea 12: 401. 1838. — Loudon, Arb. Frut. Brit. 2: 952, fig. 647. 1838. — Torr. & Gray, Fl. N. Am. 1: 594. 1840. — Chapman, Fl. South. U.S. 156. 1860. — Koch, Dendr. 338. 1869. — Gray, Man. ed. 2, 146. 1856. — Lavallée, Arb. Segrez. Enum. 114. 1877. — Dippel, Handb. Laubh. 3: 333. 1893. — Koehne, Dendr. 184. 1893; in Gartenfl. 45:

507. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 80. 1904. — Britton & Brown, Ill. Fl. 2: 186, fig. 1861. 1897; ed. 2, 232, fig. 2189. 1913. — Beadle in Small, Fl. 507. 1903; ed. 2, 506. 1913 et in Small, Man. South. Fl. 598. 1933. — Schneider, Ill. Handb. Laubh. 1: 366. 1905. — Rydb. in N. Am. Fl. 22: 206. 1905. — Syreishtchikof, Ill. Fl. Mosc. 2: 220, fig. [1.] 1907. — Standley & Calderon, Pl. Salv. 88. 1925. — Fernald, Gray's Man. ed. 8, 746. 1950. — Gleason, Ill. Fl. 2: 273. 1952.

*Philadelphus flore albo majore inodoro* Catesby, Nat. Hist. Car. 2: 84, pl. 84. 1743.

*Syringa inodora* Moench, Meth. 678. 1794.

TYPE: Catesby pl. 84. LECTOTYPE: *Harper 3353* (A).

An arching shrub, 1–3 m. high, bark of the second year's growth castaneous, exfoliating; current year's growth glabrous. Leaves ovate-elliptic or elliptic, rarely broad elliptic, subentire, faintly dentate, 5–9 cm. long, 2–3.5 cm. wide, acute or sub-cuneate rarely obtuse at the base, short acuminate at the apex, sparsely appressed pilose, rarely subglabrous above, glabrous except the primary nerves and their angles beneath. Flowers 1, 3, rarely up to 9, cymose, the pedicels, hypanthia, and sepals all glabrous; corolla disciform, 4–5 cm. across, the petals oblong, 2 cm. long, 1.5–1.8 cm. wide; stamens 60 up to 90; style equal to the longest stamens in length, glabrous, the stigmas dilated, the abaxial surface definite. Capsules subglobose-ellipsoid, 8 mm. long, 7 mm. diameter, the seeds long-caudate.

UNITED STATES: Pennsylvania: cliffs along the Delaware River, T. C. Porter, June 29, 1885 (NY), July 11, 1886 (G). Virginia: Caroline Co., Return, *Fernald, Long & Abbe 14168* (G); Polk Co., near Columbus Mountainside, *E. C. Townsend*, in 1897 (CU). North Carolina: without precise locality, *G. R. Vasey* in 1878 (US). South Carolina: Oconee Co., Tomassee Knob, *H. D. House 2070* (NY, US); Oconee County, Seneca River, *K. M. Wiegand & W. E. Manning*, August 1927 (CU). Georgia: cliffs along the Savannah River, at the Locks above Augusta, *C. S. Sargent*, March 20, 1908 (A, TOPOTYPE?); "In Georgia et Carolina circa urbem Augusta," *S. T. Olney & J. Metcalf 122* (G); Baldwin Co., Milledgeville, *T. G. Harbison 1549* (A); 1551 (A); Burke Co., *McBean, J. H. Pyron & R. McVaugh*, April 1938 (CU); Clarke Co., common on river banks, *J. H. Miller*, May 1925 (CU); Columbia Co., Lincolnton, Little River, *W. H. Duncan 9496* (CU); Dekalb Co., *John Davis 1852* (US), 7217 (BH), July 1921 (CU); Early Co., Coheelee Creek, *R. F. Thorne 7424* (CU); Early Co., Gulf Coastal Plain, *R. F. Thorne & W. C. Muenschner 8556* (CU); Macon Co., *I. Darby* in 1836 (NY); Steward Co., *R. M. Harper 1089* (NY, US); without precise locality, *Dr. Boykin* (NY). Kentucky: Scott Co., Stamping Ground, *J. W. Singer 84* (US). Tennessee: Knox Co., Knoxville, *J. N. McCarroll 42*; *A. Ruth 256* (MO, US), 260 (NY), 345 (G), 2023 (NY), May 21, 1887 (TENN), July 15, 1900 (TENN); Rutherford Co., Murfreesboro, *E. J. Palmer 35494* (A, MO, NY); Interior of Tennessee, without precise locality, Herb.



I. Carey (NY). Alabama: Dekalb Co., Mentone, *Loring* in May 1899 (US); Lee Co., Auburn, *F. S. Earle & L. M. Underwood*, April 25, 1896 (NY); Tuscaloosa Co., Brush Creek, *R. M. Harper 3353* (A,BH, G, NY, US); same county, Black Warrior River, *R. I. & E. R. Clausen*, April 1952 (CU); same locality, *E. J. Palmer 35362* (A,MO,NY,US), *35363* (A,NY); Holt, *H. E. Wheeler 1318* (A); Banks of Alabama River, *R. S. Cocks* in July 1914 (A); Bank of Chattahoochee River, *Chapman* in Dec. 1867 (NY); Without precise locality, *S. B. Buckley* in June 1841 (NY); *Chapman* (NY); Herb. P. V. LeRoy (NY).

CULTIVATED: United States: Massachusetts: Arnold Arboretum no. 15347, collected on June 30, 1913 (A), Arnold Arboretum no. 5312, collected on June 12, 1918 (BH), Aug. 8, 1918 (BH); Hort. Bot. Cambridge, *A. Rehder*, June 29, 1907 (A); Jamaica Plain, *C. E. Faxon*, June 20, 1911 (A). New York: Normal College Ground, *A.R.R.* on June 4, 1889 (NY). New Jersey: Somerset Co., Watchung, *H. N. Moldenke 1690* (NY), *2515* (BH). Pennsylvania: Delaware Co., Media, *F. W. Pennell 12976* (NY). Washington D.C.: U. S. Dept. Agri. Ground, *B. Sudworth*, May 18, 1891 (US), May 22, 1891 (US); *G. Vasey* in 1873 (US), in 1882 (US); Maryland Agri. College, *G. Vasey* in 1873 (US); Rock Creek, *L. F. Ward*, May 30, 1883 (US), May 20, 1886 (US). Missouri: Marion Co., Hannibal, Riverside Cemetery, *J. Davis 2306* (MO). Wisconsin: Green Bay, *J. H. Schuette* (NY).

*Philadelphus inodorus* has been much misinterpreted in botanical literature because of the over emphasis of various authors on the margin of the leaves and their disregard of the shape and base of the leaves and the flower characters as illustrated in Catesby's plate. Among modern collections made from southeastern United States, Catesby's illustration of the flowering and fruiting branchlets of the species is duplicated in *Palmer 25362, 35494, Harbison 1551* and *Harper 3353*, the last mentioned specimen deposited in the herbarium of the Arnold Arboretum has been selected as the lectotype for the species.

Judging from the specimens which I have examined, the Great Smokies is the center of concentration of this species. The specimens from eastern Pennsylvania, eastern Virginia, northern Kentucky and the Gulf Coastal Plain in Georgia either mark the periphery of its natural range or they were collected from escaped plants. The available field notes indicate that the habitats of *P. inodorus* Linn. are steep wooded slopes, banks of rocky streams or limestone bluffs. Duncan recorded the plant as attaining a height of eleven feet. The stems are slender and arching. The natural population flowers in middle April or early May in Georgia and Alabama. The cultivated ones bloom in middle June in Boston. Regarding the habit, Catesby remarked the plant being a small tree, rising to a height of about sixteen feet or upwards with a slender trunk. As far as I know all species of *Philadelphus* are shrubs. Catesby's remark was either due to his loose concept of the term tree or due to the crowded condition in which that particular plant grew with no chance to branch at the base.

KEY TO THE VARIETIES AND FORMS OF *P. INODORUS*

- A. Sepals glabrous outside.
- B. Leaves ovate-elliptic, elliptic or lanceolate, the base obtuse, acute or cuneate; remotely coarse-toothed.
- C. Leaves ovate-elliptic; corolla discoid.
- D. Half-open flower campanulate, the petals first suborbicular, later oblong ..... 15a. var. *grandiflorus*.
- DD. Half-open flower quadrangular, the petals first rhomboid, later orbicular ..... 15b. forma *quadranguliflorus*.
- CC. Leaves elliptic or lanceolate; corolla cruciform ..... 15c. var. *laxus*.
- BB. Leaves ovate, the base rounded; margin faintly denticulate or semi-entire ..... 15d. var. *carolinus*.
- AA. Sepals with few hairs on the outside ..... 15e. var. *strigosus*.
- 15a. *Philadelphus inodorus* var. *grandiflorus* (Willd.) Gray, Man. ed. 2, 146. 1856, ed. 4, 146. 1865; ed. 5, 166. 1867. — A. Wood, Am. Bot. Flor. 116. 1879. — Nemoto, Fl. Jap. Suppl. 294. 1936. — Fernald, Gray's Man. ed. 8, 746. 1950.

*Philadelphus grandiflorus* Willd. Enum. Pl. Hort. Bot. Berol. 511. 1809. — DC. Prodr. 3: 206. 1828. — Elliott, Sketch 1: 538. 1821. — Schrader in Linnaea 12: 395. 1838. — Sweet, Brit. Fl. Gard. ser. 2, 1: pl. 8. 1829. — Loudon, Arb. Frut. Brit. 2: 954. 1838. — Torr. & Gray, Fl. N. Am. 1: 595. 1840. — Walp. Rep. 2: 151. 1843. — Young, Fl. Texas 290. 1873. Lavallée, Arb. Segrez. Enum. 115. 1877. — Britt. & Brown, Ill. Fl. 2: 186, fig. 1862. 1897. — Nicholson, Ill. Dict. Gard. 3: 95. 1886. — Watson & Coulter, Gray's Man. ed. 6, 174. 1890. — Nicholson, Kew Hand-list 1: 225. 1894, ed. 2, 375. 1902. — Schneider, Ill. Handb. Laubh. 1: 366, fig. 234g-j, 236e. 1905. — Rydb. in N. Am. Fl. 22: 168. 1905. — Rehder, Man. Cult. Trees Shrubs 278. 1927; ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949. — Bean in Chitt. Dict. Gard. 3: 1546. 1951.

*Philadelphus speciosus* Schrader ex DC. Prodr. 3: 206. 1828; et in Linnaea 12: 43. 1838. — Koehne, Dendr. 184. 1893; in Gartenfl. 45: 507. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 80. 1904.

*Philadelphus macranthus* Jacques in Hort. Univ. 2: 17. 1841.

*Philadelphus gloriosus* Beadle in Biltm. Bot. Stud. 1: 159. 1902; in Small, Fl. 507. 1903, ed. 2, 506. 1913; et in Small, Man. South. Fl. 599. 1933. — Rydb. in N. Am. Fl. 22: 169. 1905. — Schneider, Ill. Handb. Laubh. 1: 366. 1905.

*Philadelphus columbiensis* Hort. ex Nicholson, Kew Hand-list 1: 225. 1894, ed. 2, 375. 1902, nomen nudum.

*Deutzia sanguinea* Hort. ex Nicholson, ll. cc.

*Philadelphus inodorus* sensu Gleason, Ill. Fl. 2: 273. 1952, pro parte, non Linn.

TYPE: Cultivated plant in the Botanical Garden of Berlin. LECTOTYPE: Biltmore Herb. No. 4333a, from rocky banks of Grand River, Rutherford County, North Carolina, deposited in Herbarium, Arnold Arboretum.

A mound-like shrub with slender arching branchlets, bark of two-year old growth castaneous, exfoliating; leaves ovate or ovate-elliptic, 5–11 cm. long, 2.5–5, sometimes up to 6.5 cm. wide, glabrescent or very sparsely strigose on both surfaces, bearded in the axils of primary nerves beneath, denticulate, the teeth usually coarse and remote, acute or rarely rounded at the base, acuminate at the apex; flowers ternate, solitary, or 7–9 in a true dichasium, pedicels 3–15 mm. long; sepals ovate, 8–12 mm. long, 5–6 mm. wide, acuminate; corolla campanulate at first, later semidisciform, 4–5.5 cm. across, the petals suborbicular, becoming oblong, 20–26 mm. long, 15–22 mm. wide; capsules ellipsoid, 12–15 mm. long, 6–9 mm. in diameter.

UNITED STATES: Virginia: Without precise locality, *Stebbins* (NY). North Carolina: Buncombe Co., Blue Ridge, *A. Gray* in 1843 (NY); Polk Co., Skyuka Mt., *J. R. Churchill*, May 25, 1899 (BH), same county, Pacolet River, *J. R. Churchill*, May 29, 1899 (BH, TENN); Rutherford Co., rocky banks of Grand River, near Chimney Rock, *Biltmore Herb. 4333a* (A, NY, US); same county below Hickory Falls, *Correll, Blomquist & Garren 5140* (A); mountains of North Carolina, *G. R. Vasey* in 1878 (NY); Hickory Mt. Gap, *Gray* (NY); Rutherford Gap, *S. B. Buckley*, August 1841 (NY). South Carolina: Oconee Co., along streams and rivers, *A. P. Anderson 1173* (US); Tomassee Knob, *H. D. House 2056* (NY, US); Clemson College *2116* (NY, US). Georgia: Dade Co., Lookout Mt., *E. J. Palmer 35446* (A, MO); Lookout Mt. between Tennessee and Georgia, *J. R. Churchill*, April 30, 1906 (TENN), May 3, 1906 (BH); Macon, Ocumulgee River Swamp, *J. K. Small*, May 18–24, 1895 (NY), July 8–9, 1895 (A); Rome, cliffs of Cocco, *T. G. Harbison 39* (A); same area, Black's Bluff, *Alexander, Everett & Pearson*, Oct. 1933 (NY); Sugalo River near its juncture with Senesa, *L. R. Gibbs* in 1885 (NY); Wilkes Co., Little River, *T. G. Harbison*, July 14, 1919 (A, US); without precise locality, *Herb. Chapman, 878* (US); Benton Co., Rockport, *E. B. Harger 7892* (G). Tennessee: Polk Co., *Sharp, Adams & Felix 11406* (A, TENN); Sevier Co., *H. M. Jennson 1208* (TENN). Alabama: Lee Co., Auburn, *E. T. Earle*, April 25, 1896 (US); Jackson Co., Bridgeport, *Biltmore Herb. No. 4333e* (NY); Lisbon, *C. Mohr*, July 24, 1885 (US); Mobile Co., Mobile, *E. Smith* in 1891 (A, US).

CULTIVATED: Europe: Germany: Hort. Götting, *A. Rehder 387* (A), 1644 (A); *Schrader* in 1827 (TYPE of *P. speciosus* Schrader; photograph, A). England: Kew, *Geo Nicholson 1316* (A). Asia: China: Shanghai, St. John's University, *L. H. Bailey*, May 14, 1917 (BH), May 23, 1917 (BH).

The plant cultivated in Shanghai is reported by Bailey as producing fragrant flowers.

Willdenow characterized *P. grandiflorus* by the ovate, acuminate, and dentate leaves which were fasciculate pilose in the principal nerve-angles beneath. He remarked that the plant was introduced to the Botanical Garden of Berlin as *P. inodorus*. Willdenow's concept of the species had been adopted by European botanists outside Germany for over a half century without questioning. Koch and Koehne, two outstanding German students of the genus, never accepted Willdenow's species. On observa-

tion of spontaneous material Gray found the characters used by Willdenow to be unreliable for specific distinctions and in 1856, in the second edition of his Manual of Botany, he treated Willdenow's species as a variety of *P. inodorus* Linn. This trinomial existed in Gray's Manual for over thirty years in four different editions. In 1890 when Watson and Coulter revised Gray's Manual, they re-established Willdenow's species for no obvious reasons. Meanwhile, Britton and Brown tried to distinguish *P. grandiflorus* Willd. from *P. inodorus* Linn. on the strength of the relative length of the calyx lobes, and on their geographical distribution. These authors maintained that *P. grandiflorus* Willd. had calyx lobes about twice as long as the tube and that it occurred on low ground from Virginia to Tennessee and Florida while *P. inodorus* Linn. had calyx lobes equalling the tubes and occurred principally in the mountains, from Virginia to Georgia and Alabama. This character, the proportion of sepals and hypanthium, had also been adopted for distinguishing *P. grandiflorus* Willd. and *P. inodorus* Linn. by Rydberg and Beadle. Gleason in 1952 maintained that the observations that these authors had made were not substantiated on an examination of the plant. Swinging to the other extremity, he amalgamated the two species. Fernald in 1950, in the eighth edition of Gray's Manual adopted Gray's concept, and I think he is justified in so doing.

Jacques in 1841 described a plant cultivated as *P. inodorus* in the garden of M. Bertin and named it as *P. macranthus*. He characterized that plant as having ovate-elliptic or ovate-oblong dentate leaves which are narrowed at the base, and ternate large flowers with rounded petals. Judging from his description the plant he saw must belong to *P. inodorus* var. *grandiflorus*.

Britton and Brown and Small all claimed the taxon to occur in Florida. I have seen no spontaneous specimens from that state.

Schrader in 1828 described *P. speciosus* as a plant possessing an 8-celled ovary. His illustration indicated that the cross section he made was cut through the tip of a young fruit. Due to a partial false septa projecting from the roof of each cell of the ovary such a cross section would appear 8-celled. Through the courtesy of Dr. Charles Baehni, Director of the Conservatoire et Jardin Botaniques, Genève, I have the photocopies of the original drawings and the text of Schrader's manuscript as well as the photographs of the types of Schrader's species. By the help of one of the curators of the same institution, Mr. Weibel, I received a careful description of the indumentum of the floral parts, including the hypanthium, sepals, petals, styles and disk, of all Schrader's species. I have no doubt that *P. grandiflorus* Willd. and *P. speciosus* Schrader are conspecific.

Beadle in 1902 on the strength of an abrupt contraction of the base of the capsule described *P. gloriosus* from the banks of the Coosa River near Rome in Georgia. The degree of fullness of a capsule has a profound effect on the appearance of the base of the fruit in *Philadelphus*. I have



examined many collections from the Coosa River region and found no fruit character distinctive specifically. Beadle's material appears to have fuller fruits.

15b. *Philadelphus inodorus* Linn. var. *grandiflorus* (Willd.) Gray  
forma *quadranguliflorus*, f. nov.

Frutex erectus, ramis pendulis, bienniis 5 mm. diametro, corticibus exfoliatis, hornotinis glabris; foliis oblongo-ovatis vel ovatis, 3–10 cm. longis, 1.5–5 cm. latis, basi obtusis vel rotundatis, apice acuminatis, subtiliter remoto-serratis vel subintegris, supra glabris vel adpresso-pilosis, subtus ad nervis primariis villosis barbatisque; flores 1 vel 3, raro usque ad 9, cymosis, corolla quadrangulari, petalis orbicularibus, 2.2 cm. longis, 2.6 cm. latis.

UNITED STATES: North Carolina: Rutherford Co., bank of the Broad River near Chimney Rock, Biltmore Herb. No. 6555 (NY). South Carolina: Kershaw Co. near Camden, along Wateree River, *E. J. Palmer* 39949 (A). Georgia: Rome, cliffs of Coosa River, *C. S. Sargent*, May 6, 1899 (A. TYPE).

CULTIVATED: Germany: Hort. Götting. *A. Rehder* 388 (A), 1672 (A). U.S.A.: Arnold Arboretum No. 5312, *C. E. Faxon* June 14, 1911 (A), June 16, 1911 (A). Arnold Arboretum No. 4159–2, collected on August 8, 1918 (BH); Arnold Arboretum No. 15340, collected on Oct. 3, 1916 (A); Arnold Arboretum No. 15357, collected on June 20, 1904 (A). New York: Rochester, Highland Park, *R. E. Horsey*, July 17, 1918 (BH), Sept. 4, 1918 (BH).

This form can easily be recognized by its square flowers, the petals are always broader than long and they overlap each other at anthesis. It was probably first introduced by Sargent from Georgia and distributed under the name *P. grandiflorus*. The broad petals of the flowers are very distinctive, and when the flowers first open, they appear square.

15c. *Philadelphus inodorus* var. *laxus*, comb. nov.

*Philadelphus laxus* Hort. ex Schrader in DC. Prodr. 3: 206. 1828; et in Linnaea 12: 398. 1838. — Loudon, Arb. Frut. Brit. 2: 954, fig. 677. 1838. — Lindl. in Bot. Reg. 25: pl. 39. 1839. — Lavallée, Arb. Segrez. Enum. 115. 1877. — Koehne, Dendrol. 184. 1893; in Gartenfl. 45: 507. 1896; et in Mitt. Deutsche. Dendrol. Ges. 1904(13): 79. 1904. — Rydb. in N. Am. Fl. 22: 174. 1905. — Schneider, Ill. Handb. Laubh. 1: 365. 1905. — Rehder, Man. Cult. Trees Shrubs 278. 1927; ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949. — Bean in Chitt. Dict. Gard. 3: 1546. 1951.

*Philadelphus grandiflorus* Willd. var. *laxus* (Schrader) Torr. & Gray, Fl. N. Am. 1: 595. 1840. — Walp. Rep. 2: 151. 1843. — Nicholson, Kew Hand-list 1: 225. 1894; ed. 2, 375. 1902; et Ill. Dict. Gard. 3: 95. 1886. — Anon. in Garden 40: 289. 1891. — Raffil. in Gard. Chron. III. 43: 82, fig. 36: 1908.

*Philadelphus humilis* hort. ex Schrader in DC. Prodr. 3: 206. 1928, in syn.

*Philadelphus ignea* Hort. ex Nicholson, Kew Hand-list 1: 225, 1894, in syn.

*Philadelphus pubescens* Lodd. Cat. ed. 16, 1836, nomen nudum. — Loudon, Arb. Frut. Brit. 954. 1938, in syn., non Loisel., 1820.

TYPE: *Schrader*, (Conservatoire et Jardin Botaniques, Genève).

A mound-like shrub with arching branches, the branchlets slender, pendulous, touching the ground, the bark of second year's growth ex-foliate; leaves lanceolate or elliptic-lanceolate, 4–6 cm. long, 1.5–2.5 cm. wide, cuneate or acute at the base, acuminate at the apex, glabrescent or sparsely appressed pilose above, sparsely pubescent beneath, especially along the principal nerves; beard in the nerve-axils, the margin remotely fine serrate, rarely subentire; flowers 4.5–5.5 cm. in diameter, corolla cruciform, the petals oblong, 2.3 cm. long, 1.5 cm. wide.

UNITED STATES: North Carolina: Swain Co., Nantahala Gorge, *K. M. Wiegand*, June 1931 (CU).

CULTIVATED: Europe: Switzerland, Botanical Garden of Geneva, *Schrader* (TYPE of *P. laxus* *Schrader*, photo in A); without collector, June 1826 (NY). Germany: ex. Herb. Dendrol. *Koehne* 18 (MO); Hort. Bot. Jena, *A. Rehder*, June 1895(A); Hort. Mund, *A. Rehder* 2256 (A), 2268 (A); Hort. Musk, *A. Rehder*, July 2, 1888 (A); Hannover, Bot. Garten Forstakademie, *H. Zabel*, June 13, 1894 (A). Austria: Hort. Bot. Wien, *C. Schneider*, June 6, 1902 (A). France: Segrez. Lavallée's Arboretum, June 16, 1907 (A); Les Barres, Vil-morin's Arboretum No. 7110, June 17, 1901 (A). United States: Boston: Arnold Arboretum No. 15353B, *R. B. Clark* (BH); New York: New York City, *M. Ruger* (NY); Rochester Highland Park, *R. E. Horsey*, June 16, 1918 (BH), Sept. 21, 1917 (BH); Ithaca, *Bailey*, July 5, 1916 (BH). North Carolina: Biltmore, *W. H. Manning* (BH). Tennessee: Chilhowee Park, *L. D. Greenwood* 2 (TENN). Arkansas: Hot Springs, *E. J. Palmer* 24869 (MO).

*Schrader* described *P. laxus* from a plant cultivated in the Botanical Garden of Geneva, and characterized it as having dentate leaves, which were pubescent beneath, and having solitary or ternate flowers. He gave as the origin of that taxon North America. A specimen in the Herbarium of the New York Botanical Garden which was distributed by the Geneva Botanic Garden under the name *Philadelphus inodorus* matches *Schrader*'s plate and the photograph of his type in every respect. It was collected in June 1826. As *Schrader* finished his work in 1827, this specimen was probably collected from the type plant at the time when *Schrader* made his studies. This specimen is identical with *Wiegand*'s collection made in Nantahala Gorge of North Carolina. Incidentally *Wiegand*'s collection represents the only specimen that I have examined which is not marked "cultivated." This variety differs from typical *P. inodorus* Linn. only in its narrower leaves which are sparsely pubescent beneath. As this leaf-character is not specifically distinctive, I therefore treat *Schrader*'s species as a variety of *P. inodorus* Linn.

In the Vil-morin Arboretum, Les Barres, France, a mistake was once made in recording the origin of a plant. A tag labeled "P. spec. China No. 1505" was attached to a *laxus* type of *Philadelphus*. A specimen from that plant was sent to *Koehne*, who accordingly in 1904 advanced a sup-

position that *P. laxus* Schrader was endemic to China, specifically Szechuan Province. In so doing Koehne overlooked the fact that at that early period, Szechuan, being situated in the interior region, was not accessible to Europeans. As Bretschneider remarked that during the eighteenth century and the early half of the nineteenth century, Canton was the only Chinese port open to European trade,<sup>1</sup> and *Philadelphus* does not grow in Canton, either in a wild state or in cultivation, it was highly impossible for such a plant to be introduced to Europe from China.

In the European gardens *P. inodorus* Linn. var. *laxus* S. Y. Hu existed under different binomials some of which also appear as synonyms of *P. lewisii* Pursh and *P. hirsutus* Nutt.

Torrey and Gray in 1840 interpreted Schrader's species as a variety of *P. grandiflorus* Willd. It is true that these two taxa are closely related, especially when the remotely coarse dentate leaves are considered. In this study they are both treated as varieties of *P. inodorus* Linn. The var. *grandiflorus* is distinguished by its broad ovate leaves and discoid corolla and var. *laxus* by its lanceolate or elliptic-lanceolate leaves and cruciform corolla.

#### 15d. *Philadelphus inodorus* Linn. var. *carolinus* var. nov.

*Philadelphus inodorus* sensu Sims in Bot. Mag. 36: pl. 1478. 1812. — Lavallée, Arb., Segrez. Enum. 114. 1877. — Rehder, Man. Cult. Trees Shrubs 278. 1927, ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949. — Bean, Trees, Shrubs, ed. 7, 2: 414. 1950; et in Chitt., Dict. Gard. 3: 1546. 1951, non Linn. 1753.

*Philadelphus columbarius myrtiflorus* Hort. ex Lavallée, Arb. Segrez. Enum. 114. 1877., in syn.

*Philadelphus cordatus* Hort. ex Lavallée, l. c., in syn.

*Philadelphus cordifolius* Hort. ex Lavallée, l. c., in syn.

*Philadelphus coronarius nivalis* Hort. ex Lavallée, l. c., in syn.

*Philadelphus multiflorus* Hort. ex Lavallée, l. c., in syn.

*Philadelphus floribundus* Hort. ex Lavallée, l. c., in syn., non Schrader, 1828.

*Philadelphus grahami* Hort. ex Lavallée, l. c., in syn.

*Philadelphus zeyheri multiflorus* Hort. ex Lavallée, l. c.

Frutex humilis, ramis pendulis, bienniis 2–4 mm. diametro, corticibus exfoliatis, hornotinis glabris; foliis subcoriaceis, integris vel subintegris, ovatis, 3.8 cm. longis, 2–4 cm. latis, basi rotundatis vel raro obtusis, apice breviter acuminatis, glabris vel supra sparse adpresso-pilosis et subtus ad nervis pilosis barbatisque; flores 1, vel 2, raro 3 usque ad 9, 4–6 cm. diametro, petalis suborbiculo-obovatis; staminibus 63 usque 90.

UNITED STATES: North Carolina: without precise locality, G. R. Vasey in 1878 (TYPE, US); Chimney Rock, Alexander, Everett & Pearson,

<sup>1</sup> E. BRETSCHNEIDER, History of European Botanical Discoveries in China, 155–156. 1898.

Sept. 27, 1933 (NY). Tennessee: Hamilton Co., Chattanooga, Ledges Jonas Bluff, Lookout Mountain, *S. R. Churchill* 449 (TENN).

CULTIVATED: Biltmore Herb. No. 7610 (A, G, MO, NY, US); Arnold Arboretum, *S. Y. Hu*, June 8, 1951 (A), July, 1952 (A); Arnold Arboretum No. 540-2, (Plant collected near Chimney Rock N. C.) *A. Rehder* on June 16, 1903 (MO). Arnold Arboretum No. 4159-1, collected on June 19, 1889 (A), June 26, 1902, June 28, 1904, June 14, 1911, June 23, 1916, June 26, 1916, Oct. 3, 1916 (All in A); Massachusetts Agricultural College, *C. H. Thompson*, June 7, 1921 (MO).

This variety is characterized by its ovate leaves with rounded or obtuse base and faintly denticulate or subentire margins. In nature it has very limited range of distribution. The material that I have examined all come from the mountains of western North Carolina and the adjacent southeastern Tennessee. The cultivated specimens in large American herbaria apparently all come from two sources, the one from a plant originally transplanted from the bank of the Flint River in Georgia by the Biltmore Herbarium (No. 7610), and the other from a plant originally transplanted from Chimney Rock in North Carolina as represented by the Arnold Arboretum field No. 540-2.

The introduction of this variety to European gardens was made about 1810. In 1812 a flowering specimen was presented to Sims by Wilthey of the Fulham Nursery. A colored plate was prepared from this specimen and was published under the name *P. inodorus*. A comparison of this plate with that of Catesby's reveals that those plates represent two different elements. That of Catesby depicts a plant with ovate-lanceolate leaves and oblong petals which are rounded at the apex and that of Sims' illustrates a plant with broad ovate leaves and semirhomboid petals obtuse at the apex. In this work the plant that Catesby illustrated is interpreted as the true *P. inodorus* Linn. while the plant that Sims described is identified as *P. inodorus* Linn. var. *carolinus* S. Y. Hu. Lavallée named his plant with the help of Sims' publication, thus the synonyms he listed under *P. inodorus* in the Arboretum Segrezianum are placed here as the synonyms of this variety. Rehder relied on a plant cultivated in the Arnold Arboretum for the description of *P. inodorus* in his Manual. As that plant is not a genuine *P. inodorus* Linn., Rehder's description applies only to this variety.

- 15e. *Philadelphus inodorus* Linn. var. *strigosus* Beadle in Biltm. Bot. Stud. 1: 159. 1902; in Small, Fl. 507. 1903, ed. 2, 506. 1913; et in Small, Man. South. Fl. 598. 1933. — Schneider, Ill. Handb. Laubh. 1: 366. 1905.

*Philadelphus strigosus* (Beadle) Rydb. in N. Am. Fl. 22: 168. 1905.

*Philadelphus laxis* Schrader var. *strigosus* (Beadle) Rehder in Jour. Arnold Arb. 1: 198. 1920; Man. Cult. Trees Shrubs 278. 1927; ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.



TYPE: *A. C. Hexamer* & *F. W. Maier*, June 19, 1855 (G).

A straggling shrub up to 2 m. high, bark castaneous, exfoliating; leaves ovate or ovate-elliptic, 3–7 cm. long, 2–4 cm. wide, subentire, or faintly denticulate, obtuse or rounded at the base, acuminate at the apex, glabrous or partially sparsely strigose above, uniformly strigose beneath, bearded at the nerve-angles; flowers solitary or ternate, the pedicels and hypanthia glabrous, the sepals ovate, 8 mm. long, 5 mm. wide, sparsely villose on the outside; corolla disciform, 4–5 cm. across, the petals sub-orbicular, 2 cm in diameter; stamens about 90, the longest 1 cm. long; style as long as the longest stamens, the abaxial surface of the stigma 3 mm. long.

UNITED STATES: North Carolina: Burke Co., Tablerock, *H. D. Hasse* (NY); Iredell Co., Statesville, *M. E. Hyais* 4986 (NY), May 1881 (NY). South Carolina: Kershaw Co., near Camden, *E. J. Palmer* 39949 (NY, US); Lexington Co., *A. C. Hexamer* & *F. W. Maier*, June 19, 1855 (TYPE G); Santee River, *M. Tuomey* (NY); without precise locality, *M. A. Curtis* (MO). Georgia: Richmond Co., above August, *S. T. Olney* & *J. Metcalf*, April 1855 (NY); same area, at the Locks, *C. S. Sargent* on June 20, 1908 (A); Elbert Co., *T. G. Harbison* 16 (A). Tennessee: Servier Co. *H. M. Jennison* 367 (TENN). Alabama: Montgomery Co., Montgomery, *O. L. Justice*, April 20, 1941 (CU).

CULTIVATED: Europe: Bernhard Herb (MO). U.S.: Washington: Sequim, *J. M. Grant*, June 6, 1913 (NY). Missouri: St. Louis, Missouri Bot. Gard., *J. H. Kellogg*, May 21, 1902 (CU).

Beadle was justified in treating this taxon as a variety of *P. inodorus* Linn. for it differs from the genuine species only in its thicker covering of appressed, rather stiff hairs on the lower surface of the leaves and on the exterior of the sepals. Like *P. inodorus* Linn. it has glabrous pedicels and hypanthia. In the texture, shape, and margin of the leaves, much variation exists among the specimens cited above. So far as my records go, the earliest collection was made not long before 1847 by M. A. Curtis from South Carolina. It was presented to Engelmann in 1847 under the name *P. grandiflorus* Willd. The first cultivated record that I have seen is represented by some specimens of the Bernhard Herbarium. They were then cultivated in Europe under the name *P. inodorus* Linn. or *P. laxus* Schrad.

16. *Philadelphus floridus* Beadle in Biltm. Bot. Stud. 1: 160. 1902; in Small, Fl. 507. 1903; ed. 2, 506. 1913; et in Small, Man. South Fl. 599. 1933. — Schneider, Ill. Handb. Laubh. 1: 366. 1905. — Rehder in Jour. Arnold Arb. 1: 198. 1920; Man. Cult. Trees Shrubs 279. 1927; ed. 2, 273. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949, pro parte.

*Philadelphus speciosus* sensu Lindl. in Bot. Reg. 23: pl. 2003. 1837. — sensu Rydb. in N. Am. Fl. 22: 169. 1905, non Schrader ex DC. 1828.

*Philadelphus magnificus* sensu Rehder, Man. Cult. Trees Shrubs 278. 1927, ed. 2, 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949, pro parte, non Koehne.

TYPE: Biltmore Herb. No. 11376, a flowering specimen, collected on May 3rd, 1899.

Shrub up to 3 m. high, branchlets brown, the second year's growth castaneous. Leaves ovate-elliptic or broad-elliptic, 4–10 cm. long, 2–6 cm. wide, rounded or obtuse at the base, abruptly acuminate at the apex, subentire or inconspicuously remote-serrulate, very sparsely short strigose above, uniformly strigose-villose beneath. Flowers ternate, rarely solitary, or racemose with the subsequent pairs in the axils of normal leaves, the pedicels 3–7 mm. long, glabrous or sparsely villose; hypanthia and calyx sparsely villose; sepals ovate, 7–9 mm. long, 5–7 mm. wide, acuminate; corolla disciform 4–5 cm. across, the petals suborbicular, 2–2.5 cm. in diameter; stamens 80–90, the longest 1.5 cm. long, disc glabrous, the style 15 mm. long, the stigma oar-shaped, the abaxial surface definite, 1.5 mm. long; the adaxial surface 2 or 3 times longer, diminishing gradually. Capsules ellipsoid, 1 cm. long, 9 mm. in diameter, the persistent sepals supermedian. Seeds long-caudate.

UNITED STATES: Georgia: Floyd Co., near Rome, cliffs of Coosa River, Biltmore Herb. No. 11376, flowering specimen, collected on May 3, 1899 (TYPE, photo, A, NY); same number, fruiting specimen, collected on Sept. 22, 1902 (A, NY).

CULTIVATED: Europe: England: Hort. Cantab., Pl. Loddiges in 1849 (NY). Germany: Hort. Späth ex Herb. Dendr. Schneider (A). United States: Massachusetts: Hort. Bot. Cambridge, R. Cameron, June 7, 1918 (A); Hort. Dixwell, A. Rehder, June 24, 1903 (A). Canada: Dominion Arboretum and Botanic Garden, J. M. Gillett, July 3, 1939 (A).

Lindley in 1837 prepared an illustrated account about a plant which was grown in the garden of the London Royal Horticultural Society under the name *P. grandiflorus* and he named it as *P. speciosus* Schrader. Besides reprinting Schrader's original description he made no effort to characterize that plant. From his figures we know that his plant has pubescent hypanthia and calyx, a disciform corolla with suborbicular petals. As Schrader's *P. speciosus* has glabrous hypanthia and calyx, I judge that Lindley's specimen could not be Schrader's species. To ascertain the identity of the plant which Lindley called *P. speciosus* we have to turn to his discussion for some light. In the first paragraph of his discussion he admitted that "it is hardly possible to procure the species, as defined by Professor Schrader, with certainty from the nurseries, unless from Messrs. Loddiges." In the New York Botanical Garden collection there is a specimen labeled "*P. speciosus* e. pl. Loddige." This specimen has sparsely villose hypanthia and calyx. In the form and dentation of the leaves, in the type of inflorescences, in the size of the flower and in the shape of the corolla this specimen matches Lindley's illustrations perfectly.

There is no doubt that this element was what Lindley called *P. speciosus*. It is identical with the flowering type of *P. floridus* Beadle. In preparing volume 22 of the North American Flora, Rydberg had examined this specimen. He was correct in interpreting Lindley's *P. speciosus* and Beadle's *P. floridus* as conspecific. As stated above that which Lindley interpreted as *P. speciosus* was not Schrader's species. Beadle's binomial is the oldest for this taxon.

The earliest record of its cultivation in American gardens can be drawn from two collections made by A. Rehder on June 24, 1903 in the Dixwell Garden in Jamaica Plain, Mass. Later it was also cultivated in the now extinct Cambridge Botanical Garden. The later specimen was interpreted by Rehder as *P. magnificus*.

*P. floridus* Beadle is closely related to *P. inodorus* var. *grandiflorus* (Willd.) Gray. It can be distinguished from the latter taxon by the sparsely villose hypanthia and calyx, the uniformly strigose-villose lower leaf-surfaces and the rather frequent presence of a pair of flowers in the axils of normal leaves below the terminal ternate flowers. Those characters which distinguish it from *P. inodorus* var. *grandiflorus* are also characters which link its relationship to *P. pubescens* Loisel. It is perhaps a natural hybrid of the two. Geographically this species falls into the range of *P. inodorus* var. *grandiflorus*, but its occurrence is rare. It is only known in nature by the type collections.

There are two cultivated varieties which differ from the genuine *P. floridus* by their solitary flowers, denser pubescence and smaller leaves.

#### KEY TO THE VARIETIES OF *P. FLORIDUS*

- A. Leaves 4-5 cm. long, subentire or inconspicuously remote-serrulate; hypanthia sparsely strigose-villose, the underneath tissue visible; corolla cruciform ..... 16a. var. *faxonii*.
- AA. Leaves 6-8 cm. long, prominently remote-denticulate; hypanthia densely strigose-villose, the underneath tissue obscure, corolla disciform ..... 16b. var. *rehderiana*.

- 16a. *Philadelphus floridus* var. *faxonii* Rehd. in Jour. Arnold Arb. 1: 199. 1920; Man. Cult. Trees Shrubs 279. 1927; ed. 2, 273. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.

TYPE: *C. E. Faxon*, June 28, 1907.

A graceful shrub, the bark castaneous, exfoliating; leaves elliptic, 2.5-5 cm. long, 1-2 cm. wide, obtuse or acute at the base, acuminate at the apex, subentire or faintly serrulate, glabrescent above, uniformly strigose beneath; flowers solitary or ternate, the hypanthia and calyx strigose-villose, the underneath tissue visible, the sepals ovate, 7 mm. long, 3 mm. wide, the corolla cruciform, 4 cm. across, the petals oblong, 1.8 cm. long, 1.5 cm. wide.

CULTIVATED: Boston, Mass. Hort. H. Chandler, *C. E. Faxon*, June 28, 1907 (A, TYPE); from the same plant, *C. E. Faxon*, June 16, 1911 (A).

This variety differs from typical *P. floridus* Beadle in having smaller leaves and cruciform corolla. In general appearance this variety resembles *P. inodorus* var. *laxus* (Schrader) S. Y. Hu. From the latter taxon it can readily be distinguished by its strigose-villose hypanthia and calyx. It is only known by collections made from the type plant. The Arnold Arboretum No. 10978 labeled as *P. floridus* var. *faxonii* is said to have been propagated through cuttings made from H. Chandler's garden. But the Arboretum Plant has completely glabrous hypanthia and calyx and disciform corolla with semidouble petals. It is not the genuine *P. floridus* var. *faxonii* Rehder.

16b. *Philadelphus floridus* var. *rehderianus*, var. nov.

Frutex 2 m. altus, ramis tenuibus, biennis castaneis, exfoliatis, hornotinis glabris; foliis ovatis 5–10 cm. longis, 2.5–5 cm. latis, basi acutis vel obtusis, apice acuminatis, supra sparse pilosis, subtus praesertim dense villosis, remote denticulatis; floribus solitariis, raro ternatis, pedicellis 3–8 mm. longis, dense villosis, hypanthiis calycibusque dense villosis, sepalis ovatis, 9 mm. longis, 5 mm. latis, corolla disciformi, 4–5 cm. diametro, petalis suborbicularibus, ca. 2 cm. diametro; staminibus ca. 90, 3–12 mm. longis; stylo cum stigmatibus 14 mm. longo; capsulis ellipsoideis, 10–11 mm. longis, 8–9 mm. diametro.

CULTIVATED: Arnold Arboretum No. 5311, *A. Rehder*, June 18, 1910 (TYPE, A); *C. E. Faxon*, June 14, 1911 (A), Oct. 3, 1916 (A); *C. K. Allen*, June 21, 1927 (A).

This very distinct form was introduced into cultivation through the Arnold Arboretum in 1906. It was raised from seeds collected from Highland, North Carolina by T. G. Harbison. In appearance it resembles *P. inodorus* var. *grandiflorus* f. *quadranguliflorus* S. Y. Hu. It can be readily distinguished from the latter form by its densely pubescent hypanthia and calyx and its uniformly dense pubescent lower leaf-surfaces.

The above cited specimens have been named by Rehder as *P. floridus*. The type of Beadle's species has very sparsely villose hypanthia and calyx and subentire or faintly serrulate leaves. The indumentum of the hypanthia and calyx of this variety resembles that of *P. pubescens* Loisel. It is dense and canescent. Its leaves have remote and prominent teeth. These differences are distinct enough to warrant it at least a varietal status.

Section 4. *Stenostigma* Koehne

*Philadelphus* subg. II. *Euphiladelphus* sect. 4. *Stenostigma* Koehne, emend.

*Philadelphus* Reihe 1. *Corticatae* Koehne, Deutsche Dendr. 179, 180, 1893.

*Philadelphus* Reihe 3. *Decorticatae racemosae* Koehne, op. cit. 180, 182.

*Philadelphus* sect. *Stenostigma* Koehne in Gartenfl. 45: 450. 1896; et in Mitt.



Deutsch. Dendr. Ges. 1904(13): 77, 81. 1904, pro parte. — Engler, Pflanzenf. ed. 2, 18a: 193. 1930, pro parte.

*Philadelphus Coronarii* Rydb. in N. Am. Fl. 22: 162. 1905, in clavi, s. stat.

TYPE SPECIES: *P. coronarius* Linn.

Erect shrubs with rather stiff branchlets, the bark exfoliating or closed; leaves ovate, dentate, rarely semi-entire; flowers in determinate racemes; sepals ovate; petals oblong, ovate or suborbicular; stamens 25 up to 38, rarely over 40; ovary with medianly attached placentas, the style usually divided above, the stigmas clavate, rarely spatulate or oar-shaped; capsules ellipsoid with subapical persistent sepals; seeds usually short-tailed, the lobes on the crown rounded (except some Himalayan and American species).

Geographically, this section has the widest range. Its species occur in every continent of the Northern Hemisphere. From the Ozark Plateau region northwestward to northwestern United States and the adjacent territory of Canada, and from the higher altitudes of northeastern Asia to Japan, Korea, China, the western Himalayan region, the Caucasus and southern Europe, its distribution forms a slightly discontinuous belt girdling the world. Morphologically, several of its very widely separated species such as *P. coronarius* of Europe, *P. triflorus* of the western Himalayan region, *P. tenuifolius* of northeastern Asia, *P. satsumi* of Japan and *P. lewisii* of northwestern United States are hard to distinguish. This is also true with *P. caucasicus* of the Caucasus, *P. subcanus* of Central China, *P. schrenkii* of northeastern Asia, *P. skikokianus* of Japan, and *P. gatingeri* of southeastern United States. The subdivisions of this section are here made more on the basis of geographical separations and less on morphological distinctions of the included species. They are series *Coronarii* of Europe and the Caucasus, *Tomentosi* of western Himalaya, *Delavayani* of southwestern China, *Sericanthi* of China and Korea, *Pekinenses* of north China, *Satsumani* of Japan, *Gordoniani* of northwestern United States, and *Pubescentes* of the interior low plateaus and the Ozark Plateau regions of the United States.

#### KEY TO THE SERIES

- A. Hypanthia glabrous or rarely with a few hairs at the base.
  - B. Adaxial stigmatic surface longer than the abaxial.
    - C. Seeds long-caudate, the embryos half as long as the tails (except *P. triflorus*).
      - D. Leaves glabrous or glabrescent; American species. .... Ser. 1. GORDONIANI.
      - DD. Leaves tomentose beneath; Himalayan species. .... Ser. 2. TOMENTOSI.
    - CC. Seeds medium- or short-caudate, the embryos equal to or longer than the tails.
      - D. Seeds short-caudate, the embryo longer than the tail (except *P. brachibotrys*); northern and eastern Chinese species. .... Ser. 3. PEKINENSES.

- DD. Seeds medium-caudate, the embryos equal to the tail; European and Caucasian species. . . . . Ser. 4. **CORONARI.**
- BB. Adaxial stigmatic surface shorter than the abaxial; southwestern Chinese species . . . . . Ser. 5. **DELAVAYANI.**
- AA. Hypanthia uniformly and, in general, thickly pubescent.
- B. Large shrubs up to 4 or 5 m. high; the lower surfaces of the leaves, the hypanthia and sepals uniformly long villose; southeastern United States species. . . . . Ser. 6. **PUBESCENTES.**
- BB. Medium or low shrub, 1–3 m. high; the lower surfaces of the leaves, the hypanthia and sepals strigose or scabrid (except *P. mitsai* from north-west China).
- C. Seeds short-caudate; hair on the hypanthia strigose, scabrid or villose; Chinese species. . . . . Ser. 7. **SERICANTH.**
- CC. Seeds long- or medium-caudate; hair on the hypanthia weak, short, golden, curly, only along the angles or very sparsely all over; Japanese species. . . . . Ser. 8. **SATSUMANI.**

### Series 1. **Gordoniani** (Koehne) Rehder

**Philadelphus** subg. II. **Euphiladelphus** sect. 4. **Stenostigma** ser. 1. **Gordoniani** (Koehne) Rehder, *Man. Cult. Trees Shrubs* ed. 2. 266. 1940; et *Bibl. Cult. Trees Shrubs* 191. 1949.

*Philadelphus* sect. *Stenostigma* subsect. *Gordoniani* Koehne in *Gartenfl.* 45: 450. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 77, 81. 1904, pro parte. — Engler, *Pflanzenf.* ed. 2, 18a: 193. 1930.

*Philadelphus Coronarii* Rydb. in *N. Am. Fl.* 22: 162. 1905, in clavi, s. stat., pro parte, non Koehne 1896.

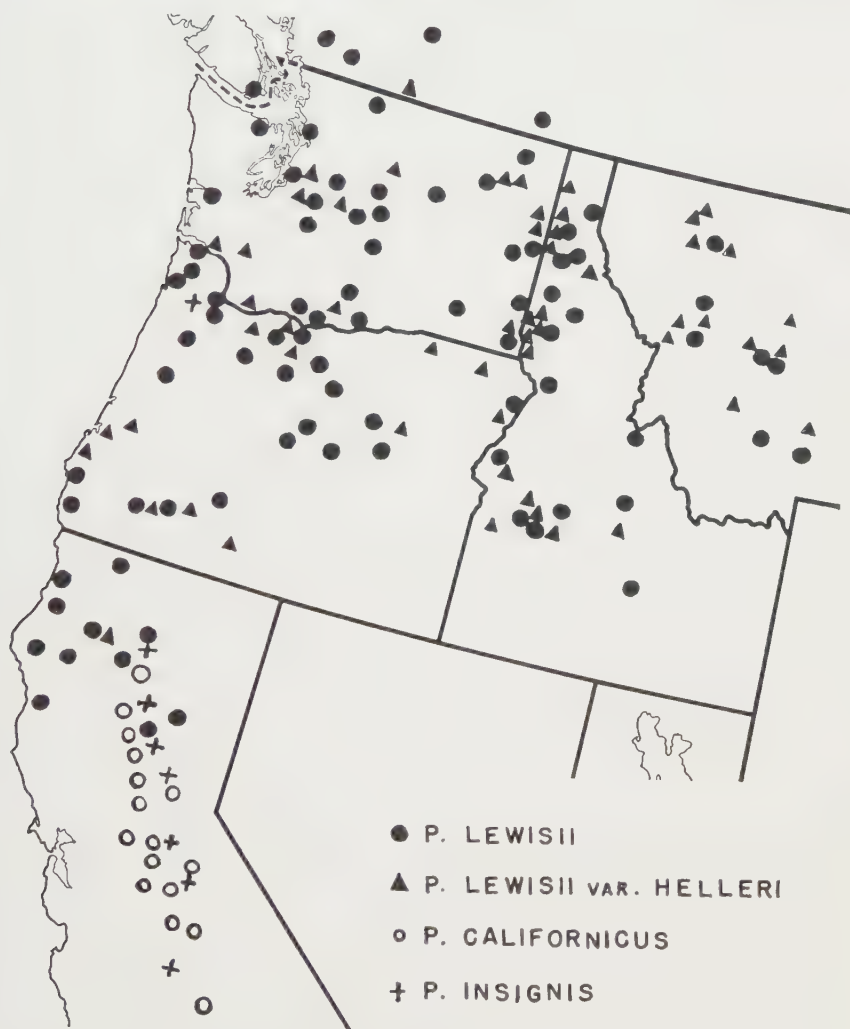
TYPE SPECIES: *P. lewisii* Pursh.

Large erect shrubs with brown or gray branchlets, the bark of the second year's growth generally closed; leaves denticulate or subentire; flowers with more or less glabrous hypanthia, the corolla usually cruciform; capsules ellipsoid with super medianly attached persistent sepals; seeds long-caudate. Four species, three in northwestern United States and adjacent Canada, and one in southern United States. Their distribution is shown in map 4.

### KEY TO THE SPECIES

- A. Petals glabrous.
- B. Disc glabrous.
- C. Anthers glabrous.
- D. Bark of the second year's growth ochraceous, brown or castaneous; western species. . . . . 17. *P. lewisii*.
- DD. Bark of the second year's growth cinereous; southeastern species. . . . . 18. *P. intactus*.
- CC. Anthers hirtellous . . . . . 19. *P. trichothecus*.
- BB. Disc pilose.
- C. Anthers glabrous; style glabrous, rim of the disk white setose. . . . . 20. *P. oreganus*.
- CC. Anthers hirtellous; style and disk pilose. . . . . 21. *P. confusus*.
- AA. Petals hirtellous on both surfaces. . . . . 22. *P. zelleri*.

17. *Philadelphus lewisii* Pursh, Fl. Am. Sept. 1: 329. 1814. — DC., Prodr. 3: 206. 1828. — Schrader in Linnaea 12: 401. 1838. — Hooker, Fl. Bor. Am. 1: 220. 1834. — Torr. & Gray, Fl. N. Am. 1: 595. 1840. — Koch in Woch. Gärtn. Pflanzenk. 2: 229. 1859. — Gray in Bot. Calif. 1: 202. 1876. — Dippel, Handb. Laubh. 3: 344, fig. 181. 1893. — Nicholson, Kew Hand-list 1: 227. 1894, ed. 2. 377. 1902. — Koehne, Deutsche Dendr. 180. 1893; in Gartenfl. 45: 541. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 81. 1904. — Schneider, Ill. Handb. Laubh. 1: 368, fig. 237, s-u. 1905. — Rydb.



MAP 4. The distribution of the species of *Philadelphus* in western United States.

in N. Am. Fl. 22: 165. 1905. — Howell, Fl. Northw. Am. 206. 1898. — Rehder, Man. Cult. Trees Shrubs 272. 1927, ed. 2, 266. 1940; et Bibl. Cult. Trees Shrubs 191. 1949. — Abrams, Ill. Fl. Pac. St. 2: 384, fig. 2304. 1944. — Bean, Trees Shrubs, ed. 7, 2: 636. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

*Philadelphus globosus* hort. ex Koch, Dendr. 344. 1869.

*Philadelphus thyrsiflorus* Hort. ex Nicholson, Kew Hand-list 1: 227. 1894; ed. 2, 377. 1902, in syn.

*Philadelphus coronarius nivalis* Hort. ex Nicholson, Kew Hand-list 227. 1894; ed. 2, 377. 1902, in syn.

*Philadelphus nivalis* Hort. ex Nicholson, ll.cc., in syn, non Jacques, 1841.

An erect shrub up to 3 m. high, the branchlets rather stiff, the second year's growth brown, rarely ochraceous or castaneous, the bark closed, with transverse cracks, slowing wearing off; current year's growth glabrous, ciliate at the nodes, buds enclosed. Leaves ovate, 4–5.5 cm. long, 2–3.5 cm. wide, rounded at the base, acute, rarely obtuse or short-acuminate at the apex, semi-entire or inconspicuously denticulate, sparsely strigose-villose on the nerves above, barbate in the nerve angles and strigose-villose on the nerves beneath, ciliate on the margins. Inflorescences 7-, 9-, or 11-flowered, rarely on weak branchlets 5-flowered, or flowers ternate or solitary, the rachis sparsely pilose or glabrescent; pedicels 2–7 mm. long, sparsely pilose, the lower ones always in the axils of normal leaves; hypanthia campanulate, glabrous; sepals ovate, 5–6 mm. long, 3 mm. wide at the base, the apex acute or acuminate; corolla cruciform, 3–4.5 cm. across, the petals oblong, 13–22 mm. long, 6–10 mm. wide, the apex rounded and emarginate; stamens 28 up to 35, the longest about half the length of the petals, the anthers oblong, glabrous; disc glabrous, the style shorter than the longer stamens, glabrous, undivided or slightly divided above, the abaxial stigmatic surface 0.5–1.8 mm. long, the adaxial surface twice as long or even longer. Capsules ellipsoid, 7–10 mm. long, 4–5 mm. in diameter, pointed at both ends, the persistent calyx super-median. Seeds long-caudate, the embryo cylindrical, 0.75 mm. long, the tail equal or twice as long, the crown with pointed lobes.

CANADA: British Columbia: Vancouver Island, Victoria, *W. R. Carter*, July 7, 1917 (G), Aug. 21, 1917 (G); *J. Macoun*, July 2, 1887 (MO, NY), Aug. 31, 1877 (NY); *C. F. Newcomber*, Aug. 14, 1916 (G), 328 (F); Fraser Valley, *Fletcher*, June 1885 (G); Sproat, Columbia River, *J. Macoun*, June 27, 1890 (US); Salmo, *F. A. MacFadden* 13915 (NY); Chilliwack Valley, *J. Macoun*, Aug. 16, 1901 (G, NY); Lake Osoyoos, *J. Macoun*, June 3, 1905 (F, NY).

UNITED STATES: Washington: Asotin Co., *C. E. Skinner* 116 (F); Chelan Co., Leavenworth, *I. C. Otis* 955 (US), *J. W. Thompson* 6734 (G), *L. M. Umbach* 482 (NY); Lake Chelan, *M. Kelly* 4 (MO); Douglas Co., Grand Coulee, *E. Mackay* 17 (G, MO, NY, US); Moses Coulee, *W. C. & M. W. Muenschner* 11253 (CU); Ferry Co., Colville Nat. Forest, *W. W. Eggleston* 10614 (US); King Co., Seattle, *L. Benson* 1154 (US), *G. Engelman & C. S. Sargent*, July 18,



1880 (A), *W. J. Eyerdam* (F), *J. G. Jack*, Aug. 18, 1904 (A), *S. M. Zeller*, Aug. 8, 1910 (MO); Kittitas Co., Rock Island, *J. H. Sandberg & J. B. Leiberg* 452 (G, NY, US); Klickitat Co., *W. N. Suksdorf* 1740 (A), 6921 (A), 7011 (A); Mt. Constitution, *H. C. Cowles* 382 (F); Olga, *C. C. Engberg*, June 19, 1905 (NY); Pierce Co., *Wiegand, Castle, Dann & Douglas* 1119 (F); San Juan Island, *C. A. Reynold* 28 (F); Spokane Co., Clark Springs, *F. O. Kreager* 598 (G, NY, US); Spangle, *W. N. Suksdorf* 300 (G); Trout Lake, Mount Rainier Forest Reserve, *J. B. Flett*, July 27, 1899 (US); Walla Walla Co., Blue Mts., *C. V. Piper*, Aug. 2, 1892 (G); same locality, *C. S. Sargent*, Aug. 1, 1896 (A); Walla Walla, *C. L. Shear* 5605 (US); Whatcom Co., *W. C. Muenscher* 7956 (G, CU); Whitman Co., Palouse, *J. G. Jack* 1294 (A); Yakima, *T. S. Brandegee* (A); same locality, *D. Griffiths & J. S. Cotton* 43 (NY, US). Oregon: Lewis River, *Lewis* (fragment of TYPE, NY); Benton Co., Brook Lane, *H. M. Gilkey*, June 16, 1943 (G); Clackamas Co., Milwaukie, *W. N. Suksdorf* 940 (A); Columbia Co., Goble, bank of Columbia River, *A. Rehder*, Aug. 22, 1904 (A); Cow Canyon Co., Madras, *M. E. Peck* 15773 (MO); Crook Co., *F. V. Coville & E. I. Applegate* 712 (A, US); same county, without precise locality, Herb. Iowa State College no. 268 (G, MO); Farewell Bend, *J. B. Leiberg* 475 (A, F, G, NY, US); Crook River, *K. Whited* 208a (A); Curry Co., *M. E. Peck* 8829 (BH, G, MO); Dalles of the Columbia River, *G. Engelmann & C. S. Sargent*, Aug. 25, 1880 (A); The Dalles, *J. W. Thompson* 2822 (MO); Farmington, *J. E. Kirkwood* 203 (NY); Forest Grove, *F. E. Lloyd*, Oct. 1849 (NY); Fort Colville to Rocky Mts., *Dr. Lyall* (G); Grant Co., Canon City, *H. E. Brown* 83 (A, MO, NY, US); Grant's Pass, *H. S. Prescott*, May 15, 1912 (G), June 8, 1912 (F); Hood River Co., *L. F. Henderson* 9207 (G, MO); E: Independence, *J. C. Nelson* 1562 (G); Jackson Co., *E. I. Applegate* 2195 (US); Josephine Co., *W. H. Camp* 49 (NY); Klamath Co., Keno, *M. E. Peck* 9418 (G, NY); Multnomah Co., Bridal Veil, *H. H. Smith* 3111 (F); Mount Hood, *H. D. Langille* in 1898 (US); Portland, *E. P. Sheldon* 12087 (F); same locality, *M. W. Gorman* 412 (US), *J. W. Thompson* 845 (MO), *L. S. Rose* 37434 (MO); Sauvie's Island, *H. F. Munroe*, June 1875 (F); Shemman Co., John Day Valley, *L. F. Henderson* 5405 (G, MO); Trail Creek Cañon, *E. P. Sheldon* 8207 (A, G, MO, NY, US); Union Co., *W. C. Cusick*, June-July 1876 (G); *J. W. Thompson* 4847 (MO); Wallowa Co., Wallowa, *M. E. Peck* 18420 (NY); Wallowa Lake, *L. Constance & C. J. Jacobs* 1416 (MO); Snake River Canyon, *Constance, Rollins, & Dillon* 1570 (G); Imnaha, *W. C. & M. W. Muenscher* 15860 (CU); Wasco Co., Hood River, *A. A. Heller* 10098 (A, G, MO, US), *E. P. Sheldon* S 12173 (F); N. W. Wheeler Co., Pine Creek, *M. E. Peck* 10051 (A, NY); without precise localities, *E. Hall* 167 (G, MO, NY), *T. J. Howell* (F), *R. D. Nevins* in 1873 (G). California: Del Norte Co., *Ruth & B. C. Maguire* 15162 (CU); Humboldt Co., Yager Road, *S. K. Harris* 3529 (G), 3530 (G); Plumas Co., *A. A. Heller* 15130 (US); Siskiyou Co., *E. E. Stanford* 1601 (MO); Trinity Co., Weaverville, *J. P. Harrington* (US); *C. Epling & W. Robison*, June 20, 1935 (MO); Yreka, *E. L. Greene*, June 24, 1876 (F, MO); without precise localities, *J. M. Bigelow* in Whipple's Exploration for a Railway Route in 1853-4 (US), *A. Kellogg & W. G. W. Harford* 247 (G, NY, US). Idaho: Boise Co., Boise, *J. A. Clark* 72 (BH, G, US), 319 (BH, G); same locality, *T. E. Wilcox* in June 1881 (G), *C. L. Hitchcock & C. V. Muhlick* 9759; Sweet, *J. F. Macbride* 1623 (F, G, MO, NY, US); Custer Co., Bear Creek, *J. F. Macbride & E. B. Payson* 3369 (G); Lake Coeur d'Alene, *Ruth & B. C. Maguire*, June 12, 1934 (CU); Pend d'Oreille, *E. L. Greene*, Aug. 8, 1889; Coeur d'Alene Mts., Carbon, *J. B. Leiberg* 1515 (US); Kootenai Co., Hope, *A. A.*

Heller 253 (F); same locality, *E. A. Mearns*, June 13, 1903 (US), *J. B. Leiberg*, July 1890 (F), July 1892 (F), *J. H. Sandberg*, July 1888 (US); Latah Co., Cedar Mt., *C. V. Piper*, July 19, 1901 (G); Clearwater River, *C. English Jr.* (BH); Viola, *D. E. Elmer* 79 (NY, US); Lemhi Co., Salmon, *E. B. & L. B. Payson* 1869 (BH, G, MO, NY); Nez Perces Co., Hatwai Creek, *Sandberg, MacDougal & Heller* 253 (CU, G, NY, US); Clearwater River, *F. G. Meyer* 879 (G); Washington Co., *M. E. Jones* 6305 (MO); without precise locality, *T. E. Wilcox* in 1883 (US). Montana: Flathead Co., Big Fork, *B. T. Butler* 2117 (NY), 2294 (NY); same locality, *L. M. Umbach*, Aug. 11, 1901 (NY); Gallatin Cañon, *J. W. Blankinship* 172 (F, US); Glacier National Park, *B. Maguire & G. Piranian* 15529 (G); Helena, *F. D. Kelsey*, June 20, 1887 (F), June 1890 (F), July 7, 1891 (F, G); Kalispell, *S. D. McKelvey*, Sept. 18, 1921 (A); Lake McDonald, *H. M. Evans*, July 16, 1924 (F); Madison Co., Pony, *P. A. Rydberg & E. A. Bessey* 4317 (F, G, NY, US); Missoula, *J. E. Kirkwood* 1151 (F, G); Bridger Mts., *W. W. Jones*, July 1905 (G); Ravalle, *C. Riss*, June 17, 1888 (A); Swan Lake, *H. N. Whitford* 18 (F); Sixteen Mile Creek, *W. M. Canby* 52b (US); without precise locality, *W. J. Howard s.n.* (G).

CULTIVATED: Europe: Kew, A. 19, *Macklearn* 429 (BH); Hort. Bot. Berol., *E. Koehne* 218 (G); Hort. Götting., *A. Rehder* 1654 (A); Plantières, *C. Schneider*, Sept. 1903 (A). United States: Arnold Arboretum 543-4 = 5876 (A), 543-5 = 15370 (A), 1004-30 (A).

This species was described on the basis of Lewis' collection made "on the Waters of Clark's River." This locality was interpreted by Piper<sup>1</sup> as the "Hellgate River, between Missoula, Mont., and the mouth of Big Blackfoot River, in Missoula county, Montana," and by Rydberg<sup>2</sup> as the "Clark's Fork of Columbia River in Montana." The label which accompanied the fragment of the type in the New York Botanical Garden gives the type locality as "Oregon, Lewis River."

Since the publication of *P. lewisii* Pursh, several binomials have been established on the strength of the pubescence of the leaves, the color of the bark of the stem, the degree of division of the style, or the shape of the apex of the sepals. The large amount of material that I have examined clearly demonstrates that none of these characters is constant and that they are unreliable for distinguishing species. The type of *P. lewisii* Pursh is a fruiting specimen. Its leaves are rather small, 2.5-4 × 1.3-2.2 cm., acute at the apex, sparsely pubescent above, and also on the nerves and in the nerve angles beneath. The apices of the persistent sepals on the fruit are acute. A large number of the specimens that match with the type in these respects have oblong petals and cruciform corollas. This character is also interpreted as typical of *P. lewisii* Pursh in this study. Specimens with obovate petals and disciform corollas are considered as a variety of *P. lewisii* Pursh. The wild populations of this species do exhibit definite patterns in the size and form of the leaves. These are treated as different forms of the typical *P. lewisii* Pursh.

*Philadelphus lewisii* has a wide range, from British Columbia down the Pacific coastal states to California and eastward to Montana and Idaho.

<sup>1</sup> C. V. PIPER, New and noteworthy plants, in Bull. Torrey Bot. Club 29: 226. 1902.

<sup>2</sup> P. A. RYDBERG, Hydrangeaceae, in North American Flora 22: 165. 1902.

In this large area it tolerates greatly varied ecological conditions. In Victoria it grows in lowland woods. In Washington it has been collected in the rocky draws among the sagebrushes. In Oregon it is found to be common in thickets, on the banks of rivers, on bluffs and in canyons. It has also been observed to grow in grassy openings associated with *Berberis* and *Quercus* in the cutover *Pseudotsuga* groves. In Idaho it occurs on cliffs and rock slides at altitudes of 900–1830 meters. Normally it grows from two up to three meters high, and its white, slightly fragrant flowers appear from late May to early July.

Although *Philadelphus lewisii* is a native of the United States, when compared with the other species cultivated in the American gardens, it is a very rare plant in this country. So far as I know, the few specimens existing in the outstanding American arboreta and botanical gardens are imported, with only one exception, from European nurseries. For example, Arnold Arboretum 5876 was imported in 1909 from the Späth nursery, and 543–5 was from Simon Louis nursery. In 1930 E. J. Palmer moved a living plant from Wolf Creek of Montana to the Arnold Arboretum (1004–30). It flowered in 1936, but has not done well in New England.

#### KEY TO THE VARIETIES OF *P. lewisii*

- A. Hypanthia completely glabrous.
  - B. Base of the leaf rounded; lamina ovate or oblong, 2–5 cm. wide (except var. *parvifolius*).
    - C. Leaves subcoriaceous, those on the flowering branches subentire or inconspicuously denticulate, the length equal to or longer than twice the width.
      - D. Petals obovate, the corolla disciform; leaves ovate or oblong-ovate.
        - E. Leaves on the flowering branches 4–6 cm. long. .... a. var. *gordonianus*.
      - EE. Leaves on the flowering branches 1–2 cm. long. .... b. var. *parvifolius*.
    - DD. Petals oblong, the corolla cruciform; leaves oblong. .... c. var. *oblongifolius*.
  - CC. Leaves chartaceous, suborbicular or broad ovate, those on the flowering shoot usually dentate or serrate, the length less than twice the width. .... d. var. *platyphyllus*.
  - BB. Base of the leaf acute; lamina lanceolate, 6–14 mm. wide. .... e. var. *angustifolius*.
- AA. Hypanthia with few hairs.
  - B. Leaves ovate or oblong, the base rounded.
    - C. Lamina 3–8 cm. long. .... f. var. *helleri*.
    - CC. Lamina 1.5–2.5 cm. long. .... g. var. *intermedius*.
  - BB. Leaves elliptic, the base acute or obtuse. .... h. var. *ellipticus*.

17a. *Philadelphus lewisii* var. *gordonianus* (Lindl.) Jepson, Man. Fl. Pl. Calif. 466. 1925. — McMinn, Ill. Man. Cal. Shrubs 139, fig. 136. 1939.

*Philadelphus gordonianus* Lindl. in Bot. Reg. 24 (Misc. Not.): 21. 1838; 25: pl. 32, 1839. — Torr. & Gray, Fl. N. Am. 1: 595. 1840. — Walp., Repert. 2: 151. 1843. — Gray, Bot. Calif. 1: 202. 1849. — Decaisne & Naudin, Man. Amat. Jard. 3: 69, fig. 19. 1868. — Lavallée, Arb. Segrez. Enum. 116. 1877. — Nicholson, Ill. Dict. Gard. 3: 95, fig. 7. 1886. — Rattan, Pop. Cal. Fl. 57. 1879, ed. 8, rev. 57. 1892. — Dippel, Handb. Laubh. 3: 342. 1893. — Koehne in Gartenfl. 45: 542. 1896. — Rydb. in N. Am. Fl. 22: 167. 1905. — Gordon in Jour. Roy. Hort. Soc. London 34: 12, fig. 6. 1908. — Mottet, Arbres Arb. Orn. Pleine Terre 224. 1925. — Rehder, Man. Cult. Trees Shrubs 272. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949. — Gilkey, Handb. Northw. Fl. Pl. 147, fig. [1]. 1942. — Abrams, Ill. Fl. Pac. St. 2: 384, fig. 2303. 1944. — Bean, Trees Shrubs ed. 7, 2: 413. 1950; et in Chitt., Dict. Gard. 3: 1546. 1951.

*Philadelphus cordatus* Petzold & Kirchner, Arb. Muscav. 203. 1864.

*Philadelphus grahami* Petzold & Kirchner, l.c.

*Philadelphus californicus* sensu Carrière in Rev. Hort. 1866: 339. 1866, non Benth.

*Philadelphus lewisii* sensu Piper in Bull. Torr. Bot. Club 29: 225. 1902, non Pursh.

*Philadelphus gordonianus* var. *columbianus* (Koehne) Rehder in Jour. Arnold Arb. 1: 196. 1919; Man. Cult. Trees Shrubs 272. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

*Philadelphus columbianus* Koehne in Gartenfl. 44: 542. 1896. — Rydb. in N. Am. Fl. 22: 166. 1905. — Schneider, Ill. Handb. Laubh. 1: 368, fig. 236, k. 1905.

TYPE: Cult. London Hort. Soc., July 9, 1838 (ISOTYPE, G).

An erect shrub; the leaves ovate, those of the vegetative shoots 5–6 cm. long, 2.5–4 cm. wide, uniformly sparsely pubescent beneath, glabrous and inconspicuously pilose along the nerves above, coarsely dentate, each side with 4 or 5 large outward pointing teeth in the middle, rounded at the base, shortly acuminate at the apex; the leaves on the flowering branch ovate, 3–5 cm. long, 1.5–3.5 cm. wide, subentire or minutely serrulate, glabrous on both surfaces, except the nerves inconspicuously pilose; hypanthia and sepals glabrous; corolla disciform, 3.5–4.5 cm. across, the petals obovate, 1.5–2 cm. long, 1.2–1.9 cm. wide, rounded at the apex; stamens ca. 35; capsules ellipsoid, 10 mm. long, 4 mm. in diameter.

UNITED STATES: Washington: W. Klickitat Co., W. N. Suksdorf, June 14, 1881 (US); Walla Walla Co., L. O. Anderson, June 8, 1883 (BH). Oregon: Curry Co., Rogue River near Elk Creek, J. B. Leiberger 4181 (US); Crook Co., Blue Mountains, W. W. Eggleston 11378 (US); Wallowa Co., near Wallowa, A. W. Sampson & G. A. Pearson 79 (US); without precise locality, T. J. Howell, July 1880 (US). California: Mendocino Co., Round Valley, V. K. Chestnut 119 (US). Montana: Big Fork, B. T. Butler 2117 (NY).

CULTIVATED: Europe: London Hort. Soc., Lindley, July 9, 1838 (G, specimen from the type plant); Hort. Bot. Berl., E. Koehne 9 (ISOTYPE of *P. columbianus* Koehne, G); Hannover, Bot. Gart. Forstakademie, H. Zabel 2 (BH), 13 (BH); Breslau, C. Baenitz, July 4, 1899 (A), June 27, 1907 (A, BH). Canada: Ottawa, Dominion Arboretum 97–485–1, M. N. Zinck 1566 (BH).



United States: Arnold Arboretum 4619 = 2221-4, *A. Rehder*, June 24, 1909 (A). New York, Rochester, Highland Park, *Mrs. R. E. Horsey*, Sept. 21, 1917 (BH), June 16, 1918 (BH).

*Philadelphus gordonianus* Lindl. was described on the basis of a living specimen raised from the seed sent to London by Douglas. A specimen collected from the type plant on July 9, 1838, is preserved in excellent condition in the Gray Herbarium. The leaves on the vegetative shoots of this specimen are pubescent and coarsely dentate. Those on the flowering shoot are subentire and glabrous. In the indumentum on the leaf-surfaces and the dentation along the margin this specimen does not differ from the typical *P. lewisii* Pursh. Nevertheless, the petals of its large flowers are broad obovate and the corolla more or less disciform. This specimen and the spontaneous material that matches with it in the disciform corolla are treated as a variety of *P. lewisii* Pursh, a species characterized by cruciform flowers. In this variety there is a considerable variation in the color of the bark of the second year's growth. The bark of the type plant is castaneous and tardily exfoliate, that of the Oregon and Montana material is reddish brown and closed, and that of the specimens from Washington and California is gray and closed. Judging from the material I have examined, this variety is very rare in American gardens.

#### 17b. *Philadelphus lewisii* var. *parvifolius*, var. nov.

Frutex parvus, ramis cinereis, bienniis castaneis, 2-3 mm. diametro, transverse rimulosis, hornotinis glabris, ad nodos ciliatis; foliis parvis, ovatis vel oblongo-ovatis, 1-2 cm. longis, 5-8 mm. latis, utrinque obtusis, raro basi rotundatis, integerrimis ciliatisque, supra glabris vel sparse pilosis, subtus glabris et in axillis nervorum barbatis; inflorescentiis 3- vel 5- raro 1-floris, rhachibus 5-10 mm. longis, pedicellis pilosis, hypanthiis glabris; sepalis ovatis, acutis; corolla disciformi, 1.5-2 mm. diametro, petalis oblongo-obovatis, 7-10 mm. longis, 5-8 mm. latis, apice rotundatis, staminibus ca. 30; disco glabro, stylo 5 mm. longo,  $\frac{1}{3}$ - $\frac{1}{2}$  divisio, stigmatibus clavatis; capsulis ignotis.

UNITED STATES: M o n t a n a : Missoula, *J. E. Kirkwood* 1151 (TYPE, F; fragment A; MO, ISOTYPE); Helena, *B. T. Butler* 865 (NY).

This variety is distinguished by its small habit, entire, oblong-ovate leaves and small, very much crowded flowers. In appearance it reminds one of the hybrid *P. lemoinei*, but this hybrid and its various forms all have pubescent, broad-ovate, serrate, or elliptic-lanceolate leaves. The type of this variety was collected in the prairie of Missoula. Mr. M. Canoso of the Gray Herbarium knows that country well, and he assures me that it is a spontaneous plant. Doubtlessly it is closely related to Nelson's *P. intermedius*, but the original description of the latter calls for broad-ovate, short-petiolate, or subsessile leaves and "foliose-bracted" flowers. Nelson cited no specimens. My material which fits his description has sparsely puberulous hypanthia.

17c. *Philadelphus lewisii* var. *oblongifolius*, var. nov.

A typo recedit foliis oblongis vel oblongo-ellipticis, 4–6.5 cm. longis, 1.3–3 cm. latis, utrinque obtusis vel interdum apice acutis, integris vel raro inconspicuis crenatis; hypanthiis glabris, sepalis ovato-lanceolatis; corolla disciformi, 3–4 cm. diametro, petalis oblongis, 1.5–2 cm. longis, 1 cm. latis, apice erosis, subrotundatis; disco et stylo glabris.

UNITED STATES: Washington: Chelan Co., Wenatchee, *K. Whited* 143 (US), 1175 (US); Whitman Co., Wawawai, *C. V. Piper* 3838 (G, NY; US, TYPE); Seattle, *C. A. Mosier* (US); Yakima region, North Fork, *J. Cotton* 465 (US); Rattlesnake Mountain, *J. Cotton* 674 (G, US). Oregon: Jackson Co., Wimer, *E. W. Hammond* 123 (US). California: Humboldt Co., Valley of the Van Duzen River, *J. P. Tracy* 2886 (US); Hupa Indian Reservation, *H. P. Chandler* 1333 (G, NY, US).

This variety is distinguished from the typical *P. lewisii* by its oblong or oblong-elliptic leaves with obtuse bases. Its flowers are large, and its introduction into cultivation is desirable.

17d. *Philadelphus lewisii* var. *platyphyllus* (Rydb.), comb. nov.

*Philadelphus platyphyllus* Rydb. in N. Am. Fl. 22: 167. 1905.

*Philadelphus gordonianus* sensu Abrams, Ill. Fl. Pax. St. 2: 384. 1944, pro parte, non Lindl.

TYPE: California, Mt. Shasta, *H. E. Brown* 562 (NY).

Bark of the second year's growth gray, closed, the current year's growth glabrous; leaves broad elliptic or suborbicular, rarely ovate, 4.5–7 cm. long, 2.5–5 cm. wide, rounded at the base, acute at the apex, coarsely dentate or subentire, glabrous or rarely sparsely pilose above, bearded and more or less glabrous beneath; inflorescences 5-, 7-, or 9-flowered, the lower pairs in the axils of normal leaves; pedicels, hypanthium and calyx glabrous, the sepals ovate-elliptic, 6 mm. long, 3 mm. wide; corolla cruciform, 3.7–4.5 cm. across, the petals oblong-obovate, rounded at the apex; stamens ca. 38, the longest 7–9 mm. long; disc and style glabrous, the latter 4 mm. long, the stigma oar-shaped.

UNITED STATES: Washington: Cape Horn, *C. V. Piper* 5031 (G, US); Klickitat Co., *W. N. Suksdorf* 6641 (NY), 6922 (NY). California: Siskiyou Co., south side of Mt. Shasta, *H. E. Brown* 562 (NY, TYPE; US, ISOTYPE); Trinity Co., *W. H. Brewer*, 1864 (US); without precise locality, *A. Kellogg & W. G. W. Harford* 247 (NY). Idaho: without precise locality, *F. V. Coville & T. H. Kearney Jr.* 234 (US). Montana: Big Fork, *B. T. Butler* 547 (NY).

This variety can be distinguished from the typical *P. lewisii* Pursh and other related forms by its large, broad-elliptic or suborbicular, chartaceous leaves. Rydberg considered it a species. As there is no essential difference between this taxon and *P. lewisii* Pursh other than the texture and general appearance of the leaves, I think it warrants no higher rank than a variety.

Rydberg recorded the type as *Brown* 561. But the type material de-

posited in the New York Botanical Garden, as well as the isotypes in the United States National Herbarium, all have the number 562 on the labels. This discrepancy is apparently a clerical error.

17e. *Philadelphus lewisii* var. *angustifolius* (Rydb.), comb. nov.

*Philadelphus angustifolius* Rydb. in N. Am. Fl. 22: 166. 1905.

*Philadelphus gordonianus* sensu Abrams, Ill. Fl. Pac. St. 2: 384. 1944, pro parte, non Lindl.

TYPE: Washington, *Mrs. Bailey Willis*, in 1883 (NY).

Bark of the second year's growth castaneous, exfoliate or tardily exfoliate, the current year's growth sparsely pilose; leaves lanceolate, 3–4.5 cm. long, 6–14 cm. wide, acute at the base, shortly acuminate at the apex, glabrous (except the nerves) on both surfaces, subentire or inconspicuously serrulate with one or two teeth on each side; inflorescences, 5-, 7- or rarely 9-flowered, the lower pairs in the axils of normal leaves; hypanthium and calyx glabrous; corolla cruciform, 3 cm. across, the petals oblong, 1.3 cm. long, 5–7 mm. wide, the apex rounded; disc and style glabrous, the stigma oar-shaped.

UNITED STATES: Washington: Palace Camp, *Mrs. Bailey Willis*, in 1883 (NY, TYPE); Tacoma, *Mrs. Bailey Willis*, in 1883 (NY).

This narrow-leaved variety is known only from the type collection. It is very distinct because of its lanceolate leaves. As the width of the leaves is regarded as an insufficient specific character for the northwestern American *Philadelphus*, this taxon is treated as a variety of *P. lewisii* Pursh.

17f. *Philadelphus lewisii* var. *helleri* (Rydb.), comb. nov.

*Philadelphus helleri* Rydb. in N. Am. Fl. 22: 166. 1905.

TYPE: Idaho: *A. A. & Gertrude Heller* 3374 (NY).

Bark of the second year's growth brown, castaneous, or cinereous, closed with transverse cracks, the current year's growth sparsely pilose, glabrescent; leaves oblong-ovate or ovate, glabrous or along the nerves or near the base sparsely pilose, 3–6 cm. long, 1.5–2.8 cm. wide, rounded at the base, acute or rarely obtuse at the apex, subentire or inconspicuously serrulate; inflorescences 7- or 9-, rarely 5-flowered, the lowermost pair in the axils of normal leaves; hypanthium and sometimes the calyx sparsely pilose; corolla cruciform, 3–4 cm. across, the petals oblong, the apex obtuse or rounded; disc and style glabrous.

CANADA: British Columbia: Gale, *G. Engelmann & C. S. Sargent*, July 23, 1880 (A); between Cascade and Rossland, *J. W. Thompson* 14415 (A, MO, NY); Oliver, *O. J. Murie* 1189 (MO); Nelson, *J. Fletcher* 621 (MO).

UNITED STATES: Washington: Asotin Co., bank of Snake River, *C. L. Hitchcock et al.* 8367 (BH, G); Chehalis Co., Satsop, *A. A. & G. Heller*

4023 (F, G, US); Chelan Co., *E. A. Purer* 7790 (MO); Cowlitz Co., *F. V. Coville* 703 (US); Ferry Co., Boulder Creek, *W. W. Eggleston* 10621 (US); King Co., *Savage, Cameron & Lenocker*, June–July 1898 (F); *C. A. Mosier*, June 8, 1892 (US); Kittitas Co., *A. D. E. Elmer* 380 (NY, MO, US); Ellensburg, *K. Whited* 518 (US), *J. W. Thompson* 6721 (G, MO); Muckleshoot Prairie, *Dr. Ruhn* (F, G); Palouse, *J. G. Jack* 1367 (A, US); Spokane Co., *Dr. Holmes* 966 (NY, US), *J. G. Jack* 1402 (A), 1418 (A), 1457 (A, US), *C. V. Piper* (NY); without precise locality, *G. R. Vasey* 349 (G). Oregon: Columbia River banks, *H. Y. Edward*, July 1873 (NY); Blue Mountain Springs near Prairie City, *M. E. Peck* 10318 (A); Coos Co., *W. Hayon* in 1911 (F); Columbia Co., *Goble, J. G. Jack*, Aug. 22, 1904 (A); Dayville, *W. E. Lawrence* 1014 (US); Hood River, *C. S. Sargent*, Aug. 14, 1896 (A); Jackson Co., *C. L. Hitchcock & J. S. Martin* 4983 (NY), *E. W. Hammond* 123 (MO); Klamath Co., *E. R. Kalmbach* in 1939 (US); Minam River, *E. P. Sheldon* 9047 (A, NY, US); Multnomah Co., *J. Howell*, June 1879 (A); Wallowa Co., Imnaha National Forest, *F. V. Coville* 2416 (US); Imnaha, *M. E. Peck* 17657 (NY); Wallowa Lake, *C. L. Shear* 5612 (US); Wasco Co., Cow Canyon, *F. V. Coville & E. I. Applegate* 675 (US); data on localities not clear, *W. C. Cusick* 106 (F), *J. Howell* in 1880 (US); *J. T. Jardine* 65 (US). California: Along Eel River, *B. Davy & W. C. Blasdale* 5547 (US); without precise locality, *G. R. Vasey* in 1875 (US). Idaho: Boise Co., *Muhlick* 9759 (NY); bank of Boise River, *J. A. Clarke* 319 (F, MO); *C. N. Woods & I. Tidestrom* 2586 (US); Bay Horse, *L. F. Henderson* 3795 (US), *J. S. Newberry*, Aug. 1881 (NY); Canyon Co., Big Willow, *J. F. Macbride* 102 (G, MO, NY, US); Lake Coeur d'Alene, *Capse, G. B. Aiton* 3091 (NY, US); Coeur d'Alene, *H. J. Ruth* 125 (US); Idaho Co., Salmon River, *W. C. & W. W. Muenscher* 15414 (CU); Kootenai Co., St. Maries, *H. D. House* 4927 (US); Latah Co., Moscow, *L. Abrams* 839 (A); *J. G. Jack* 1287 (A), 1289 (A), *M. Murley* 1734 (NY); Nez Perces Co., Lake Waha, *A. A. & G. Heller* 3347 (NY, TYPE; F, MO, ISOTYPES); Hatwai Creek, *Sandberg, MacDougal & Heller* 253 (G, NY, PARATYPES of *P. confusus* Piper); Nez Perces Reservation, Lewiston, *A. A. Heller*, May–June 1892 (F); same locality, *L. F. Henderson* in 1894 (US); without precise locality, *J. H. Sandberg*, June 1892 (G, NY); Priest Lake, *D. T. MacDougal* 175 (NY); Shoup, *J. F. Kemp* 65 (NY); Shoshone Co., *E. J. Palmer* 37804 (A, MO); Washington Co., Ruth Creek, *M. E. Jones* 6305 (NY); without precise locality, *G. Ainslie* in 1874 (US). Montana: Bear Gulch, *E. W. Scheuber*, July 17, 1901 (F, NY); Beartown, *E. Scheuber*, July 18, 1901 (NY); Beaverhead Co., Pioneer Range, *C. L. Hitchcock & C. V. Muhlick* 13026 (BH, MO); Flathead Co., Big Fork, *B. T. Butler* 7026 (NY); Columbia Falls, *J. G. Jack* 1575 (A), *S. D. McKelvey*, Sept. 20, 1921 (A); Flathead Lake and vicinity, *Mrs. J. Clemens* (F), *H. T. & J. M. Roger* 1056 (MO, NY); Gallatin Co., Gallatin Cañon, *F. Tweedy* 1261 (NY); Granite Co., *C. L. Hitchcock & C. V. Muhlick* 14414 (MO); Lewis & Clark Co., Wolf Creek, *E. J. Palmer* 36963 (A, MO, NY, US); Lake St. Marz, *S. D. McKelvey*, Sept. 9, 1921 (A); Lost Horse, *J. B. Leiberger* 2918 (US); Missoula Co., Flackfoot, *W. G. Chapman* 26 (NY); Missoula, *C. L. Hitchcock & C. V. Muhlick* 9090 (NY); Head of Jocko River, *C. S. Sargent*, July 15, 1883 (A); The Lo-Lo, *M. J. Elrod* 127 (MO, NY), Lolo National Forest, *E. J. Palmer* 37770 (NY, MO, US); Mission Mts., *D. T. MacDougal* 526 (NY, US); Ravalli Co., *C. L. Hitchcock & C. V. Muhlick* 14520 (MO); Silver Bow Co., *F. Tweedy* 66 (NY); Swan Lake, *J. G. Jack* 2376 (A); Tenderfoot, *R. S. Williams*, July 31, 1891 (NY).



**CULTIVATED:** Europe: Hort. Göttingen, *A. Rehder* 402 (A). Canada: Ottawa, Dominion Arboretum 09-147-2, *J. M. Gillett* 7131 (A), 7133 (BH). United States: Arnold Arboretum 543, without collector, July 4, 1890 (A), Sept. 19, 1890 (A), June 29, 1910 (A); same stock, *W. N. Manning* in 1923 (BH); Arnold Arboretum 543-3 = 5876, without collector, June 30, 1913 (A); Arnold Arboretum, *E. J. Palmer*, June 18, 1936 (A). Washington, D.C., *G. R. Vasey*, June 4, 1879 (US). Rochester, Highland Park, *Mrs. R. E. Horsey*, June 17, 1918 (BH), Sept. 4, 1918 (BH).

This variety differs from typical *P. lewisii* Pursh only in the presence of some hairs on the hypanthium and calyx. It is more commonly met with in American gardens than the typical *P. lewisii*. Besides the stocks imported from European nurseries in the late 1800's, it was independently transplanted from California to Washington by Vasey and from Montana to the Arnold Arboretum by Palmer.

17g. *Philadelphus lewisii* var. *intermedius* (Nelson), stat. nov.

*Philadelphus intermedius* Nelson in Bot. Gaz. 42: 53. 1906.

LECTOTYPE: Idaho, *J. F. Macbride & E. B. Payson* 3037 (US).

Bark of the second year's growth castaneous, closed, transversely rimulose, tardily wearing off; the current year's growth sparsely weak villose, later glabrescent; leaves broad ovate, 1.5-2.5 (rarely up to 3 cm.) long, 8-15 (rarely up to 22 mm.) wide, rounded at the base, acute or obtuse at the apex, entire or faintly denticulate with one or two teeth on each side, hirtellous on both surfaces or glabrescent; inflorescences 3-, 5-, rarely 7- or 9-flowered, the lower pairs in the axils of normal leaves; hypanthia and sepals sparsely pilose; corolla subdisciform, 2.5 cm. across, the petals ovate, 9-10 mm. long, 7-8 mm. wide, the apex rounded; stamens ca. 35; disc and style glabrous.

UNITED STATES: Oregon: Wallowa Co., Jim Creek, *E. P. Sheldon* 8283 (A, NY). Idaho: Blaine Co., Martin, *J. F. Macbride & E. B. Payson* 3037 (US, LECTOTYPE; MO). Montana: Bitterroot Valley, *S. Watson* 138 (G, US).

When Nelson published *P. intermedius*, he cited no specimen. According to his description his taxon represents a small-leaved form with broadly oval to ovate, shortly petiolate or subsessile leaves rounded at the base, and foliose-bracted flowers. *Macbride & Payson* 3037 seems to fit that description best. This collection has sparsely pilose hypanthia and calyces. It is selected to represent the type of this small-leaved pubescent variety.

17h. *Philadelphus lewisii* var. *ellipticus*, var. nov.

Frutex, ramulis brunneis, hornotinis sparse pilosis, glabrescentibus; foliis ellipticis 4-7 cm. longis, 2-3.5 cm. latis, utrinque acutis, raro apice breviter acuminatis, chartaceis, subintegris vel remote inconspicuo-denticulatis, supra glabris raro sparse pilosis, subtus ad nervos strigoso-pilosis, barbatis; inflorescentiis, 5-, 7-, raro 9-floris; hypanthiis sparse pilosis;

sepalis ovatis, 4–6 mm. longis, acutis vel acuminatis; corolla cruciformi, 3.5 cm. diametro, petalis oblongis, 14–16 mm. longis, 7 mm. latis, glabris; staminibus ca. 30, antheris glabris; disco et stylo glabro.

CANADA: British Columbia: Vancouver Island, Saanichton, *I. Mounce*, July 7, 1939 (NY); Victoria, *J. Macoun* 231 (G, NY, US), 86468 (NY).

UNITED STATES: Washington: Chelan Co., Wenatchee Mountains, *J. W. Thompson* (A, G); Klickitat Co., Major Creek, *W. N. Suksdorf* 1741 (A); Spokane Co., N. Spokane, *J. G. Jack* 1456 (A), *F. O. Kreager* 31 (G, NY, US); Wahkiakum Co., Altoona, *W. N. Suksdorf* 6815 (A); Wawawai, Snake River, *E. R. Lake*, July 4, 1892 (F, US). Oregon: Birch Bay, *Dr. Holmes*, in 1838–42 (NY, US); Douglas Co., *L. F. Ward* 56 (NY, US); Grant Co., Grant's Pass, *Munson Hopkins*, Aug. 31, 1889 (US); Jackson Co., Walker Creek, *E. I. Applegate* 2341 (US); Klamath Co., *F. V. Coville & E. I. Applegate* 269 (A, TYPE; US, ISOTYPE); Klamath Falls, *E. I. Applegate* 184 (G, US); Spencer Creek, *E. I. Applegate* 2085 (US); Klamath Indian Reservation, *F. V. Coville* 1522 (US); Lake Chalan, *M. W. Gorman* 628 (US); Portland, *F. A. Walpole* 272 (US); Umatilla Co., Pilot Rock, *W. W. Eggleston* 12671 (US). California: Humboldt Co. or Mendocino Co., *H. N. Bolander* (G, US); Laytonville, *A. Eastwood* 9308 (BH); Fieldbrook, *J. P. Tracy* 8646 (A); Trinity Co., *L. Benson* 2194 (MO, NY, US). Idaho: Benton Co., Priest River, *C. C. Epling* 7929 (US); Coeur d'Alene Mountains, Clark's Fork, *J. B. Leiberger* 1666 (US); Nez Perces Co., *W. W. Eggleston & H. St. John* 21991 (US). Montana: Columbia Falls, *J. G. Jack* 2419 (A), *R. S. Williams* 678 (US); Flathead Lake, *M. C. Jones* 8370 (US).

18. *Philadelphus intectus* Beadle in Biltm. Bot. Stud. 1: 160. 1902. — Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 82. 1904. — Rydb. in N. Am. Fl. 22: 167. 1905. — Schneider, Ill. Handb. Laubh. 1: 368. 1905. — Beadle in Small, Fl. 507. 1903, ed. 2, 507. 1913; et in Small, Man. South. Fl. 599. 1933.

*Philadelphus pubescens* var. *intectus* (Beadle) A. H. Moore in Rhodora 17: 123. 1915. — Rehder, Man. Cult. Trees Shrubs 273. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

*Philadelphus sanguineus* Hort. ex Nicholson, Kew Hand-list ed. 2, 377. 1902. in syn.

TYPE: Tennessee, Nashville, Biltmore Herb. 11378 (photo & fragment A, NY).

An erect tall shrub up to 5 m. high, the branches cinereous, the second year's growth 3–4 mm. in diameter, the bark closed, the current year's growth glabrous, the nodes not ciliate. Leaves ovate or oblong-elliptic, those on the vegetative shoot 6–9.5 cm. long, 4–6 cm. wide, those on the flowering shoot 3–6 cm. long, 1.5–3.5 cm. wide, rounded or obtuse at the base, acuminate at the apex, the acumen 5–10 mm. long, glabrous on both surfaces, remotely and finely serrulate along the apical half of the margin, ciliate; petioles 4–7 mm. long, sparsely ciliate. Inflorescences 5-, 7-, or 9-flowered, the lower pairs in the axils of normal leaves; pedicels 4–6 mm.

long, glabrous; hypanthia campanulate, glabrous; sepals ovate, 6 mm. long, caudate at the apex; corolla disciform, 3 cm. across, the petals oblong-obovate, 15 mm. long, 12 mm. wide, the apex rounded and erose; stamens ca. 38; disc and style glabrous, stigmas spatulate, the adaxial surface three times longer than the abaxial. Capsules subglobose ellipsoid, 5–7 mm. long, 4–5 mm. in diameter, the persistent calyx subapical. Seeds medium- or long-caudate, the embryo 1.25 mm. long, the tail as long or a little shorter.

UNITED STATES: Kentucky: Lyon Co., Kuttawa, *W. W. Eggleston* 4544 (NY). Tennessee: Nashville, Bluff of the Cumberland, Biltmore Herb. 11378 (fragment and photo of TYPE, A, NY), 11378c (TOPOTYPE, NY); same locality, *C. D. Beadle*, June 1899 (A, very likely an ISOTYPE), *T. G. Harbison* 67 (A). Oklahoma: Le Flore Co., Page, *E. J. Palmer* 21623 (A, NY, US).

CULTIVATED: Europe: Villa Thuret, May 30, 1889; Hort. Bot. Berol. 10, *E. Koehne*, June 19, 1894 (G), July 10, 1895 (G), Sept. 3, 1894 (G). United States: Arnold Arboretum 4454, without collector, Sept. 10, 1913 (A); 4454–2, *A. Rehder*, July 18, 1918 (A); 539–6 = 15339, without collector, June 30, 1913 (A), Sept. 10, 1913 (A), same number, *A. Rehder*, July 1, 1916 (A); 15358, *E. J. Palmer*, June 11, 1936 (A), 15376, *C. K. Allen*, June 21, 1927 (A); 1052–36, *E. J. Palmer*, Oct. 3, 1940 (A), June 24, 1943 (A).

*Philadelphus intactus* Beadle was described on the basis of a specimen collected on the bluffs of the Cumberland River below Nashville. Beadle's detailed description portrays the type exactly. Its completely glabrous leaves and hypanthia suggest a close relationship with *P. lewisii* Pursh. Its stiff upright tall habit and its ovate or oblong-elliptic leaves resemble those of *P. pubescens* Lois. Moore maintained that the differences between *P. pubescens* Lois. and *P. intactus* Beadle are comparable to those between *P. coronarius* Linn. and *P. tomentosus* Wall. As he accepted the combination *P. coronarius* var. *tomentosus* (Wall.) Hook. f. & Thom., he also established the trinomial *P. pubescens* var. *intactus* (Beadle) Moore. Rehder differs from Moore in keeping *P. coronarius* Linn. and *P. tomentosus* Wall. as distinct species but accepted Moore's interpretation of treating *P. intactus* Beadle as a variety of *P. pubescens* Lois. As there is actually a closer tie between *P. intactus* Beadle and *P. lewisii* Pursh than between the former and *P. pubescens* Lois., I can see no justification in keeping it as a variety of the last-named species.

*Philadelphus intactus* was introduced into cultivation long before it was properly named. Villa Thuret received seeds from C. S. Sargent labeled *P. hirsutus* in the 1880's. In the Botanical Garden of Berlin a plant interpreted by Koehne as *P. gordonianus* was under cultivation before the 1890's. The same taxon was distributed by the Späth and other nurseries as *P. "sanguineus"* and *P. "latifolius verrucosus."* In the United States specimens represented by these trade names were introduced by the Arnold Arboretum around 1910, and they were numbered in the field 4454–2 and 539–6. Meanwhile in the Cambridge Botanical Garden a plant of the same

species was cultivated under the name *P. hirsutus*. Cuttings from this plant were planted in the Arnold Arboretum under the field number 15358. It is very likely that both the European stock and the Cambridge planting of this species were introduced into cultivation by Gattinger, who practiced medicine in eastern Tennessee in the late 1800's and botanized that area very extensively. Some of his collections of a vegetatively similar species were labeled and distributed in outstanding American herbaria as *P. hirsutus*. Again in 1905 T. G. Harbison went to the type locality to collect specimens and seeds for the Arnold Arboretum. Specimen number 4454 was raised from Harbison's seeds.

18a. *Philadelphus intactus* var. *pubigerus*, var. nov.

Frutex altus, ramulis cinereis vel plumbeis, hornotinis glabris; foliis ovatis vel ellipticis, supra glabris vel glabrescentibus, subtus uniforme strigoso-villosis, subintegris vel utrinque 1 vel 2 dentibus minutis; inflorescentiis 7- vel 9-floribus, paribus inferioribus in axillis foliorum positis; hypanthiis sepalisque glaberrimis, capsulis obovoideo-ellipsoideis; seminibus longicaudatis.

UNITED STATES: Arkansas: Baxter Co., Norfolk, *D. Demaree* 3071 (MO, US); Garland Co., Hot Springs, *E. J. Palmer* 26870 (A, MO); Le Flore Co., Page, *E. J. Palmer* 22623A (A, TYPE); Logan Co., Magazine Mountain, *D. Demaree* 17727 (MO), 21320 (NY); Marion Co., Rush, *E. J. Palmer* 6033 (A, MO); Pope Co., London, *H. E. Wheeler*, May 10, 1922 (F); Van Buren Co., Shirley, *E. J. Palmer* 25202 (A, MO).

This variety is distinguished from the typical *P. intactus* Beadle by its pubescent leaves. In this respect it resembles *P. pubescens* Lois., but the latter species has pubescent hypanthia. Besides this morphological differentiation existing between this pubescent variety and the typical glabrous *P. intactus*, there is also a geographical separation between them. *Philadelphus intactus* was discovered on the steep rocky slopes and bluffs of the Cumberland River, and its present range is in the interior low plateau region, principally in the Nashville Basin and the Lexington Plain. *Philadelphus intactus* var. *pubigerus* is restricted to the interior highland region. It occurs on the rim of bluffs on the top of Magazine Mountain or on the rocky bluffs of the Ouachita River. Geographically it is more closely associated with *P. pubescens* than with *P. intactus*. Morphologically it serves as a link between these two species and a bridge between the *Gordoniani* series of the northwestern states and the *Pubescentes* series of the southeastern states of the United States.

19. *Philadelphus trichothecus*, sp. nov.

Frutex erectus, ramulis brunneis, bienniis 2–3.5 mm. diametro, cortice clauso, hornotinis strigoso-pilosis; foliis ovatis vel oblongo-ellipticis, 3–7 cm., raro usque 8.5 cm. longis, 1–3 cm. latis, basi rotundatis vel obtusis, apice breve acuminatis, acutis vel raro obtusis, supra ad nervos pilosis, aliter glabris, subtus barbatis et ad nervos strigoso-pilosis, subintegris vel



utrinque 2- usque 6-dentatis; inflorescentiis 5-, 7-, raro 3-floribus, bracteis foliaceis; hypanthiis sparse pilosis, sepalis ovato-oblongis, 8 mm. longis, basi 3.5 mm. latis, apice caudatis; corolla cruciformi, 3-4.5 cm. diametro, petalis oblongis, 17-20 mm. longis, 8-10 mm. latis, glabris; staminibus ca. 30. antheris hirsutis; disco et stylo glabris; capsulis obovoideis, 7 mm. longis, 6 mm. diametro; seminibus ignotis.

CANADA: British Columbia: Vancouver Island, Victoria, Oak Bay, *W. R. Carter* (G, TYPE); Fraser River at Hope, *C. L. Hitchcock & J. S. Martin* 7361 (MO, NY).

UNITED STATES: Washington: Ferry Co., Columbia River below Kettle Falls, *H. T. Roger* 558 (G, MO, NY); Klickitat Co., Bingen, *W. N. Suksdorf* 3704 (A); Mt. Constitution, *H. C. Cowles* 382 (G); Whatcom Co., *W. C. & W. W. Muenscher* 5430 (BH). Oregon: Clear Water, *Rev. Spalding*, May 28 (G); Portland, *F. A. Walpole* 2 (US); Oneonta Tunnel, *J. W. Thompson* 4710 (MO, US), Wasco Co., near Rice Station, *W. E. Lawrence* 122 (BH). California: Humboldt Co., Willow Creek, *L. R. Abrams* 7200 (NY); Siskiyou Co., *G. D. Butler* 1558 (MO, US); Trinity Co., Weaverville, *J. P. Harrington*, June 2, 1928 (US). Idaho: Boise River, *A. I. Mulford*, July 1892 (NY); Nez Percés Co., *J. H. Sandberg*, June 1892 (G); Capse, *G. B. Aiton* (MO). Montana: Garnet Co., *Mrs. E. W. Scheuber* 193 (F, NY, US).

CULTIVATED: Arnold Arboretum 22652, *R. B. Clark*, June 19, 1941 (BH).

Both in leaf form and in the sparsely pilose hypanthia this species resembles *P. lewisii* var. *helleri* (Rydb.) S. Y. Hu, but it can readily be distinguished from the latter taxon by its hirsute anthers.

20. *Philadelphus oregonus* Nuttall ex Torr. & Gray, Fl. N. Am. 1: 595. 1840, in syn., *nomen nudum*.

*Philadelphus gordonianus* sensu Torr. & Gray, l.c., pro parte, quoad spec. Nuttall, non Lindley.

TYPE: Oregon woods, *Nuttall* (G).

Frutex erectus, ramulis brunneis, bienniis 3-4 mm. diametro, cortice clauso, hornotinis sparse pilosis, glabrescentibus; foliis late ellipticis, ovato-ellipticis vel ovatis, 5-8 cm. longis, 2-4.5 cm. latis, basi obtusis vel rotundatis, apice obtusis vel acutis, subintegris, supra sparse strigoso-pilosis, subtus praeter nervos glabris; inflorescentiis 7-, 9- vel 11-floribus, paribus inferioribus in axillis foliorum compositis, pedicellis 3-5 mm. longis, glabris; hypanthiis sparse pilosis; sepalis ovatis, 7 mm. longis, apice acuminatis; corolla cruciformi, 3.5 cm. diametro, petalis oblongis, apice rotundatis, 1.5 cm. longis, 1 cm. latis; staminibus ca. 35; margine disci solis vel disco et stylo pilosis; capsulis ellipsoideis, 7 mm. longis, 5 mm. diametro; seminibus longicaudatis.

UNITED STATES: Oregon: Portland, *A. Eastwood* 1132 (A); Oregon woods, *Nuttall* (G, TYPE; NY, ISOTYPE). California: Humboldt Co., Arcata, *A. A. Heller* 13776 (MO, NY, US); Dyerville, *H. H. Smith* 3928 (F, G,

NY, US); Trinity Co., Rush Creek, *H. S. Yates* in June 1914 (US). Idaho: Lake Pend d'Oreille, *E. L. Greene*, Aug. 8, 1889 (US).

21. *Philadelphus confusus* Piper, Bull. Torr. Bot. Club 29: 225. 1902. —Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 81. 1904. —Schneider, Ill. Handb. Laubh. 1: 367. 1905. —Rydb. in N. Am. Fl. 22: 166. 1905. —Rehder, Man. Cult. Trees Shrubs 272. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

TYPE: Washington, Tum-Tum Mountain, *O. D. Allen* 221 (G).

An erect shrub, the second year's growth brown, 2–4 mm. in diameter, the bark closed, with few transverse cracks, the current year's growth glabrous, ciliate at the nodes. Leaves ovate-elliptic, 4–7 cm. long, 2–3 cm. wide, obtuse at both ends, subentire, glabrous on both surfaces except the principal nerves. Inflorescences 5-, 7-, rarely 3-flowered, the lower pairs in the axils of normal leaves; hypanthia subglobose, glabrous, the sepals ovate, 5–6 mm. long, acute at the apex; corolla cruciform, 2.5 cm. across, the petals oblong, 15 mm. long, 6 mm. wide, glabrous, the apex rounded; stamens ca. 25, anthers hirtellous at the base; disc sparsely pilose, style very short, with the stigmas 4 mm. long, spatulate. Capsules broad-ellipsoid, 6–8 mm. long, 5–6 mm. in diameter, the persistent calyx supermedian. Seeds long-caudate, the embryo cylindrical, 0.75 mm. long, the tail slightly longer.

UNITED STATES: Washington: King Co., Issaquah, *J. W. Thompson* 10522 (A, MO); Cascade Mountains, *Dr. Lyall* 1859 (G); Tum-Tum Mountain, *O. D. Allen* 221 (G, TYPE; A, MO, NY, US, ISOTYPES). California: Humboldt Co., Yager Road, *S. K. Harris* 3529 (G); *H. H. Smith* 3928 (G, MO). Idaho: Latah Co., Moscow, *M. Murley* 1734 (MO).

It is fitting to call this species *P. confusus*. There is no strong character to warrant it a distinct species, yet it is hard to amalgamate it with the other known species. It was described on the basis of three collections, namely, *Allen* 221 from Washington, *Sandberg, Heller and McDougal* 253 from Idaho, and *Brown*, July 16, 1896, from Oregon. *Brown*'s collection, with its glabrous hypanthium, disk and anthers, is typical *P. lewisii* Pursh. *Sandberg, Heller and McDougal* 253 represents a mixture of fruiting and flowering material collected from different places as well as on various occasions. Some specimens of this number are *P. lewisii* and others are *P. lewisii* var. *helleri*. *Allen* 221 was designated as the type of the species. A year after the publication of the species, on the sheet deposited in the Gray Herbarium, Piper wrote, "This I made the type of *confusus* relying principally on the style character. I now regard this as unreliable and think the leaf pubescence furnishes on the whole the best distinction between *gordonianus* and *lewisii*. Dentation, style and bark characters seem to me more inconstant." Thus Piper invalidated his species. Rydberg and Rehder accepted this species, distinguishing it from *P. lewisii* by its yellowish or gray closed bark and acute sepals. Again these are variable characters. By employing a good binocular, hairs are observed on the style,

disk, and anthers of the type material. This suggests its relationship with *P. oreganus* Nutt., which has a pubescent disc, and *P. trichothecus* S. Y. Hu, which has hirtellous anthers.

## 22. *Philadelphus zelleri*, sp. nov.

Frutex erectus, ramulis brunneis, bienniis 3 mm. diametro, cortice clauso, hornotinis sparse villosis; foliis ovato-ellipticis, 3–6 cm. longis, 1.5–3 cm. latis, basi obtusis, rotundatis vel acutis, apice acutis vel breviter acuminatis, utrinque praeter nervos glabris; inflorescentiis 7- vel 9-floribus; hypanthiis calycibusque sparse pilosis; sepalis ovatis, 5–6 mm. longis, apice acutis; corolla cruciformi, 3–5 cm. diametro, petalis obovatis, utrinque hirtellis, 16–18 mm. longis, 9–10 mm. latis, apice erosis; staminibus ca. 35, antheris hirtellis; disco et stylo sparse pilosis; capsulis ignotis.

UNITED STATES: Washington: San Juan Island, Friday Harbor, S. M. & E. B. Zeller 974 (US, TYPE; fragment, A).

This is a very strange specimen. Of all the northwestern American material I have examined, this is the only one which has hirtellous petals. Its hirtellous anthers suggest a close relationship with *P. trichothecus* S. Y. Hu, but it can easily be distinguished from the latter species by its pubescent petals.

## Series 2. *Tomentosi*, ser. nov.

### *Philadelphus* subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 2. *Tomentosi*, ser. nov.

*Philadelphus* sect. *Stenostigma* subsect. *Satsumari* Koehne in Gartenfl. 45: 451, 561. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 82. 1904, pro parte.

*Philadelphus* sect. *Coronarii* (Koehne) Nakai in Bot. Mag. Tokyo 29: 64. 1915, pro parte.

*Philadelphus* ser. *Coronarii* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949, pro parte.

TYPE SPECIES: *P. tomentosus* Wall. ex G. Don.

Frutices erecti, foliis ovatis, apice caudatis vel acuminatis, acumine 1.5–2.5 cm. longo, floribus racemosis, paribus inferioribus in axillis foliorum positis; corolla parva, 2–3 cm. diametro; staminibus 25 usque 38; stylo  $\frac{1}{3}$ – $\frac{1}{2}$  diviso, faciebus stigmatum ventralibus saepe fissis; capsulis ellipsoideis vel obovoideis; caudis seminum brevibus vel elongatis.

This series is isolated in a small area of the western Himalayan region between Long. 77–79° E. and Lat. 30–33° N. There is no geographical isolation among the three included species. They all occur along the roads on the forested slopes at altitudes of 2000 to 3000 meters.

## KEY TO THE SPECIES

A. Style glabrous.

B. Leaves tomentose beneath; seeds with long tails; hypanthia often with

- few weak caducous villose hairs. . . . . 23. *P. tomentosus*.  
 BB. Leaves glabrous beneath; seeds with short tails; hypanthia glabrous. . . . . 24. *P. triflorus*.  
 AA. Style pubescent. . . . . 25. *P. lancifolius*.

23. *Philadelphus tomentosus* Wall., Num. List, No. 3653. 1831, *nom. nud.* — G. Don, Syst. 2: 807. 1832, *descr.* — Royle, Ill. Bot. Himal. 1: 215. 1835; 2: *pl.* 46, *fig.* 1, 1839. — Loudon, Arb. Frut. Brit. 2: 955. 1838. — Walp., Repert. 2: 151. 1843. — Dippel, Handb. Laubh. 3: 338, *fig.* 177. 1893. — Koehne, Deutsche Dendr. 182. 1893; in Gartenfl. 45: 562. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Schneider, Ill. Handb. Laubh. 1: 371, *fig.* 237c-e. 1905. — Osmaston, For. Fl. Kumaon 230. 1927. — Rehder, Man. Cult. Trees Shrubs 275. 1927, ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Engler, Pflanzenf. ed. 2, 18a: 194. 1930. — Bean, Trees Shrubs ed. 7, 2: 420. 1950; et in Chitt., Dict Gard. 3: 1547. 1951.

*Philadelphus nepalensis* Wall. ex Loud., Hort. Brit. 196. 1830, *nom. nud.* — (*P. nipaulensis*) G. Don, Gen. Syst. 2: 807. 1832, in syn.

*Philadelphus coronarius* var. *tomentosus* Hook. f. et Thom. in Jour. Linn. Soc. Bot. 2: 83. 1857. — Maxim. in Mém. Acad. Sci. St. Pétersb. VII. 10 (16): 41 (Rev. Hydr. As. Orient. 41). 1867. — Clarke in Hook. f., Fl. Brit. Ind. 2: 407. 1878.

TYPE: *Wallich 3653A* (*Thomson* from Gassain, Kew).

Shrub 2–3 m. high, bark of second year's growth cinnamon, tardily exfoliating; current year's growth glabrous or glabrescent, 1.5–2 mm. in diameter. Leaves ovate, rarely lanceolate, 4–10 cm. long, 2–5 cm. wide, rounded or obtuse at the base, caudate at the apex, the acumens 1.5–2.5 cm. long, 5- or 7-nerved, glabrescent above, uniformly villose beneath, the trichomes compressed. Inflorescences pseudoracemose, 5- or 7-, rarely 3-flowered, the lower pairs usually in the axils of normal leaves, bracts to the terminal flowers often leafy, linear or lanceolate, up to 4 cm. long, 1 cm. wide, rather persistent; pedicels 6–11 mm. long, villose, hypanthium and calyx more or less glabrous, often with weak caducous villose hairs; sepals ovate, 5 mm. long, 3 mm. wide, acuminate; corolla cruciform, 1.5–2.5 cm. across, the petals obovate-oblong, 0.5–1 cm. long, 5–8 mm. wide; stamens about 25, the longest 8 mm. long; disk glabrous, the style 7 mm. long, the upper one third divided, the stigma clavate, the abaxial surface definite, 1–1.5 mm. long, the adaxial surface 3 or 4 times longer, often split at the middle. Capsule ellipsoid, 1 cm. long, 6–7 mm. in diameter, the persistent sepals supermedian. Seeds with medium-long tails.

INDIA: Chamba State: Camba Range, *R. N. Parker*, June 6, 1919 (A); Pangi, June 1919 (A); Alwas, *R. R. Steward* 2512 (A, NY). Garhwal: Panikhanada, Phagti, *A. E. Osmaston* 382 (A); same area, *H. Falconer* 470 (G, NY). Siwalik & Jaunsar Divisions: *Chakrata Amar Chand* 44 (NY). Kumaon: *R. Strachey & J. E. Winterbottom*, C (G). Kulu Himalaya: Puling, *W. Koelz* 284 (NY). Himal. Bor. Occ. Regio



Temp.: *T. Thomson*, alt. 7–10,000 ft. (G, NY); *T. Thomson*, alt. 6–9000 ft., A (G).

CULTIVATED: Europe: Kew, *G. Nicholson* 1317. United States: Arnold Arboretum nos. 15419 (= 2482–2 — from Germany), 4785 (from Kew), 15422 (4785–3) (all in A).

One of the Thomson collections and the Strachey and Winterbottom collection both represent mixtures of different elements in the Gray Herbarium. On the Thomson sheet there are two specimens. "A" represents a shoot with three fruits. Its leaves are tomentose and it belongs to this species. "B" is a flowering specimen of *P. triflorus* Wall. Its leaves are glabrous beneath, except the principal nerves, which are sparsely villose. The Strachey & Winterbottom sheet has three elements. A is a fruiting specimen. B and C are flowering specimens. The lower surface of the leaves of A and B is glabrous, except the principal nerves, beneath. They are *P. triflorus* Wall.

*Philadelphus tomentosus* Wall. was established on the basis of three collections from Gassain, Simore, and Kumaon of the western Himalayan region. It was validated by G. Don's description published in 1832. According to this description, the species has ovate acuminate leaves which are tomentose beneath. I have not seen the syntype. Among the more recent collections, the specimens that fit Don's description in the leaf character all have more or less glabrous hypanthia, low stamen count, glabrous disk and style, clavate stigma with the abaxial surface often split, ellipsoid fruit, and long-tailed seeds.

*Philadelphus tomentosus* Wall. is restricted to the western Himalayan region. Koehne in 1904 recorded it from Japan. There is some mistake in his identification. In the western Himalayan region the plants occur generally in shady forests at altitudes of 2100–2800 meters. The white, fragrant flowers appear in May in some areas and in June or July in other places.

According to Loudon, *P. tomentosus* Wall. was introduced into cultivation in 1822. It is a species with comparatively small flowers. Among the cultivated examples I have seen material prepared from the Arnold Arboretum, Kew, Hort. Plantières, Hort. Les Barres, Hort. Späth, etc. According to my understanding of the species, only the material from the first two institutions is true to the type of the species.

24. *Philadelphus triflorus* Wall., Num. List 3653. 1831, *nomen nudum*. — Royle, Ill. Bot. Him. 1: 215. 1835, *nomen subnudum*. — Loudon, Arb. Frut. Brit. 2: 955. 1838, in syn. — Koch in Wochenschr. Gärtn. Pfl. 2: 228. 1859, in syn.

*Philadelphus nepalensis* Koehne, Dendr. 183. 1893; in Gartenfl. 45: 618. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 85. 1904. — Schneider, Ill. Handb. Laubh. 1: 373, fig. 238g. 1905. — Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 192. 1949, non Wall. ex Loudon 1830.

TYPE: *Wallich 3653B* (Kew).

Erect shrub, bark of the second year's growth light brown, tardily exfoliating, the current year's growth glabrous. Leaves ovate, 6–9 cm. long, 3–5 cm. wide, rounded or obtuse at the base, caudate at the apex, the acumen 15–25 mm. long, glabrous above, entirely glabrous or the principal nerves sparsely pubescent beneath. Inflorescences racemose, 5- or rarely 3- or 7-flowered, the lower pairs in the axils of the normal leaves, the bracts of the terminal flowers linear or narrow-lanceolate, up to 3 cm. long, 4 mm. wide; pedicels (5-) 10–15 mm. long, glabrous or glabrescent; hypanthium and calyx glabrous; sepals ovate, 5 mm. long, 3 mm. wide, acuminate at the apex; corolla subdisciform, 2–3 cm. across, the petals ovate, 1–1.4 cm. long, 0.8–1.2 cm. wide; stamens 35–38, the longest 8 mm. long; disc and style glabrous, the latter 6 mm. long, the upper one third or half divided; stigma clavate, the abaxial surfaces 1.5 mm. long, the adaxial ones slightly longer, split. Capsules obovoid, 8 mm. long, 6 mm. in diameter, the persistent sepals subapical. Seeds with very short tails, the testa fuscous, reticulate, and more or less rugose.

NORTHERN INDIA: Chamba State: between Kukti and Hursa, *W. Koelz 867* (NY). Punjab: Bashahr State, Simla district, in forest at Bhali, *R. N. Parker 3034* (A); near Sangla, *M. V. Laurie 3579* (A); Kulu, *W. Koelz 1981* (NY). Garhwal: Tihri, Jumna Valley, data on label obscure (A). Kumaon: *Wallich 3653C* (*R. Brown*, Kew); *R. Strachey & J. E. Winterbottom* (A, BH, G). Himal. Bor. Occ. Regio Temp.: *T. Thomson* (BH, G). Simore: *Wallich 3653B* (TYPE, Kew).

CULTIVATED: Europe: Hort. Bot. Berol., *E. Koehne 467* (A, G, ISOTYPE of *P. nepalensis* Koehne); Hort. Münkau, *A. Rehder 405* (A); Hort. Späth, *C. K. Schneider* in 1902 (A). United States: Arnold Arboretum 6004, *C. E. Faxon*, June 21, 1910 (A), June 14, 1911 (A); *A. Rehder*, July 18, 1918 (A), June 30, 1920 (A); Arnold Arboretum 15419 = 810-42, *S. Y. Hu*, June 13, 1951 (A).

When Wallich first recorded the Himalayan *Philadelphus*, he cited three collections under two binomials, *P. tomentosus* and *P. triflorus*. His list number 3653A was from Gossainthan, 3653b from Simore, and 3653C from Kumaon. G. Don validated *P. tomentosus* Wall. in 1832 by giving it a description in which he characterized that species as having ovate leaves which are acuminate, denticulate, and tomentose beneath. In 1835 Royle doubtfully suggested *P. triflorus* Wall. as a juvenile form of *P. tomentosus* Wall. From that time *P. triflorus* Wall. has been treated as a synonym of *P. tomentosus* Wall. In 1893 Koehne described *P. nepalensis* on the basis of a plant cultivated in the Botanical Garden in Berlin, and characterized it as a species with leaves glabrous except the principal nerves beneath. A few years later, in a discussion about that species, he suggested that *P. triflorus* Wall. might belong to the same taxon. If this is true, the glabrous Himalayan species should be called *P. triflorus* Wall. and not *P. nepalensis* Koehne, for the latter binomial is preoccupied. Through the kindness of Dr. N. L. Bor, Assistant Director of the Royal Botanic Gardens,

Kew, this supposition has been confirmed. Dr. Bor kindly asked Mr. L. L. Forman to examine the specimens of *Philadelphus* in the Wallich herbarium for me. According to his report *Wallich 3653A*, a fruiting specimen, labeled *P. tomentosus* Wall., has leaves pubescent below. This specimen should be the type of the species as validated by G. Don. *Wallich 3653B*, labeled *P. triflorus* Wall., has leaves, hypanthium, style and disk all glabrous. Thus there is no doubt as to what Wallich meant for *P. triflorus*. It is different from *P. tomentosus* Wall. and conspecific with *P. nepalensis* Koehne. Mr. Forman also remarked that *Wallich 3653C*, another fruiting specimen, labeled *P. tomentosus* Wall., has glabrous leaves and it appears to equal *3653B*.

This species is undoubtedly closely related to *P. tomentosus* Wall. Geographically and ecologically they cannot be separated. But morphologically *P. triflorus* Wall. has leaves glabrous beneath. At first I suspected the glabrous Himalayan element to be a variety of *P. tomentosus* Wall. But when I saw the very short-tailed seed of a specimen with glabrous leaves, I inclined toward keeping it as a distinct species. In a seed of *P. tomentosus* Wall. the testa is ochraceous and the tail is as long as the embryo. In *P. triflorus* Wall. the testa is fuscous and the tail is one fourth the length of the embryo.

This species has long been cultivated in Europe. *Rehder 405* was collected as early as 1888. In American gardens some specimens of this species are cultivated under the name *P. tomentosus*. The plants distributed by the Park Department of Rochester under the name *P. "magnificus"* definitely belong here.

The cultivated specimens all have castaneous exfoliating branchlets and the axils of the principal nerves barbate. In this respect they differ slightly from the spontaneous material, which has light brown bark and glabrous nerve angles beneath.

25. *Philadelphus lancifolius* Koehne in *Gartenfl.* 45: 561. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904 (13): 82. 1904. — Engler, *Pflanzenfam.* ed. 2, 18a: 194. 1930.

TYPE: *C. B. Clarke 46543* (British Museum).

Shrub with grayish brown bark on the second year's growth. Leaves ovate or ovate-lanceolate, 4–7 cm. long, 1–3 cm. wide, caudate, the acumen about 2 cm. long, dentate, with 3–7 teeth on each side, 7-nerved, the lower surface thickly tomentose. Inflorescences pseudoracemose, 7- or 9-flowered, loose, the lower pairs in the axils of normal leaves. Flowers not known. Fruiting pedicels 1–1.5 cm. long; capsules obovoid, about 8 mm. long, 6 mm. in diameter, the persistent sepals super-medial, the remaining basal portion of the style pubescent (according to Koehne). Seed not seen.

NORTHERN INDIA: Kumaon: *R. Blinkworth*, ex Herb. *C. B. Clarke 46543* (photograph of TYPE, A).

The foregoing description is a synthesis of characters that can be detected from a photograph of the type and those given by Koehne. In describing

the shape of the leaves Koehne used the words "länglich oder länglich-lanzettlich." I do not choose to employ the English equivalents of these words, for the leaves in the photograph of the type appear ovate or ovate-lanceolate to me.

The type is a fruiting specimen with the capsules all open and the styles broken off. Koehne observed hairs on the remaining basal portion of the style. By this character of the hairy style *P. lancifolius* Koehne is distinguished from its closely related species *P. tomentosus* Wall. *Philadelphus lancifolius* Koehne is known only from the type collection. Among all the Himalayan material that I have examined, I have seen no specimen with pubescent style. Although molds have been mistaken for hairs by eminent botanists, I hesitate to doubt Koehne's observation, for individuals with a pubescent style have been found in the natural populations of many regions, and they may also occur in western Himalaya. According to my understanding of the permanence of the styler hairs in species like *P. schrenkii* Rupr., I know that although the hairs are delicate, they are persistent and can be observed even on mature fruit. If the species does have a pubescent style, even though Koehne's material is rather advanced in age, his observation was not impossible.

### Series 3. *Pekinenses*, ser. nov.

#### *Philadelphus* subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser 3. *Pekinenses*, ser. nov.

*Philadelphus* sect. *Stenostigma* subsect. *Coronarii* Koehne in Gartenfl. 45: 451, 596. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904, pro parte.

*Philadelphus* sect. *Coronarii* (Koehne) Nakai in Bot. Mag. Tokyo 29: 64. 1915, pro parte.

*Philadelphus* ser. *Coronarii* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.

TYPE SPECIES: *P. pekinensis* Rupr.

Frutices saepe humiles, foliis ovatis vel ovato-ellipticis, apice acuminatis; inflorescentiis 5- usque 7-floris, hypanthiis glabris; corolla praesertim parva, 2-3 cm. (raro 3.5 cm.) diametro; staminibus 25 vel 30, raro plus; disco et stylo glabris, stigmatibus spatulatis vel clavatis, faciebus dorsalibus brevissimis; capsulis subglobosis vel ellipsoideis; seminibus breviter vel mediano-caudatis.

Species of this series are concentrated in the North China uplands, including Johel, Hopei, Shansi, Shensi, and southern Kansu, and north-western Hupei. One species occurs in the hills outside Nanking, and its variety is found in the uplands of western Chekiang, Kiangsi and southern Anhwei.

#### KEY TO THE SPECIES OF THE SERIES

- A. Seeds very shortly caudate, the tails shorter than the embryo; capsules subglobose, the persistent sepals apical; rachis 0.2-1.5 cm. long; leaves glabrous on both surfaces. . . . . 26. *P. pekinensis*.



- AA. Seeds medium caudate, the tail as long as the embryo; capsules ellipsoid, the persistent sepals supermedian; rachis 2–12 cm. long; leaves strigose on the principal nerves beneath.
- B. Leaves very sparsely strigose above; style spatulate, the tail of the seed as long as the embryo; bark of the second year's growth brownish gray, closed. . . . . 27. *P. brachybotrys*.
- BB. Leaves uniformly setose above, the trichomes compressed; style clavate; the tail of the seed half as long as the embryo; the second year's bark castaneous, exfoliate. . . . . 28. *P. laxiflorus*.

26. *Philadelphus pekinensis* Ruprecht in Bull. Phys.-Math. Acad. Sci. St. Pétersb. 15: 365. 1857; et in Mém. Biol. 2: 543. 1858. — Koehne in Gartenfl. 45: 597. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Bretschneider, Hist. Eur. Bot. Discov. China 349, 1054. 1898. — Schneider, Ill. Handb. Laubh. 1: 373, fig. 273, *p-r* et 238, *e-f*. 1905. — Silva Tarouca, Freidland-Laubgeh. 283, fig. 351. 1913; et 255, fig. 309. 1930. — Nakai in Bot. Mag. Tokyo 29: 65. 1915; et Fl. Sylv. Kor. 15: 50. 1926. — Limpricht in Fedde, Repert. Sp. Nov. Beih. 12: 402 (Bot. Ergeb. Reis. Hochgeb. Chin. Ost.-Tib.). 1922. — H. H. Hu, Ic. Pl. Sin 1: 29 1927. — Rehder in Jour. Arnold Arb. 5: 151. 1924, 8: 113. 1927, 12: 275. 1931; Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 193. 1949. — Liu in Bull. Pek. Soc. Nat. Hist. II. 3: 104. 1925. — Minami, List Pl. Manch. Mong. 183. 1926. — Chen, Ill. Man. Chin. Trees Shrubs 373, fig. 279. 1937. — Kitagawa, Lin. Fl. Mansh. 253. 1939. — Sata, Ill. Manch. Mong. Trees ed. 2, 128. 1943. — Bean, Trees Shrubs ed. 7, 2: 417. 1950; et in Chitt, Dict. Gard. 3: 1546. 1951.

*Philadelphus coronarius* sensu Turcz. in Bull. Soc. Nat. Moscou X. 7: 151. 1837. — Maxim. in Mém. Div. Sav. Acad. Sci. St. Pétersb. 9: 471 (Ind. Fl. Pekin.). 1859, non Linn. 1753.

*Philadelphus coronarius* Linn. var. *pekinensis* Maxim. in Mém. Acad. Sci. St. Pétersb. Ser. VII. 10 (16): 42 (Rev. Hydrang. As. Or. 42). 1867. — Franch. in Nouv. Arch. Mus. Hist. Nat. Paris II, 6: 5 (Pl. David. 125). 1883. — Forbes & Hemsl. in Jour. Linn. Soc. Bot. 23: 278. 1887.

*Philadelphus parviflorus* Carr. in Rev. Hort. 1870: 460. 1870.

*Philadelphus rubricaulis* Carr. in Rev. Hort. 1870: 460. 1871. — Bretschneider, Hist. Eur. Bot. Discov. China 830. 1898. — Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 193. 1949, ? in syn.

*Deutzia chaetii* Lévl. in Fedde, Repert. Sp. Nov. 9: 451. 1911. — Rehder in Jour. Arnold Arb. 12: 275. 1931, in syn.

TYPE: *P. Y. Kirilov*, hills west of Pekin (Herb. Acad. Sci. St. Pétersb.).

A graceful, low, compact shrub up to 2 m. high, bark of second year's growth castaneous, exfoliating; current year's growth glabrous. Leaves ovate, those on the sterile shoot 6–9 cm. long, 2.5–4.5 cm. wide, obtuse or rounded at the base, long-acuminate at the apex, the acumen 2–2.5 cm. long, serrate, glabrous on both surfaces, occasionally bearded in the nerve

axils beneath, 5-nerved; those on the flowering shoot 3-4, rarely up to 7 cm. long, 1.5-2.5 cm. wide, glabrous on both surfaces, bearded in the axils of the principal nerves beneath, serrate, rarely subentire. Inflorescences 5-, 7-, 9-, rarely 3-flowered, the lowest pair of flowers often in the axils of normal leaves, the rachis 2-15 mm. long, the bracts linear, 3-4 mm. long, 0.5 mm. wide, ciliate, the pedicels 3-6 mm. long, glabrous; hypanthium and calyx glabrous; sepals ovate, 4 mm. long, 2.5 mm. wide, acuminate; corolla discoid, 2-3 cm. across, the petals obovate, 9-11 mm. long, 8 mm. wide; stamens 25, the longest 5-7 mm. long; disk and style glabrous, the style 4-5 mm. long, the upper one fifth to one fourth divided, the stigma subspatulate, the apical end enlarged, the abaxial surface short and broad, 1 mm. long, the adaxial ones three times as long. Capsules subglobose or obconic, 5-7 mm. in diameter, the persistent sepals subapical. Seeds short-tailed.

CHINA: *Johel*: *A. David* 2219 (G); *Wei-chang, Wm. Purdom* 83 (A). *Hopei (Chihli)*: Peking and vicinity, Western Hills, *J. Hers*, 2515 (A), 2225 (A); *Po-hau-shan, J. Hers* 1462 (A), 1680 (A); same locality, *W. Y. Hsia* 2144 (NY); *Miao-feng shan, J. Hers* 2539 (A); *Peking & Kalgan Road*, hills near Great Wall, *J. G. Jack*, Oct. 5, 1905 (A); *Kalgan Valley, F. T. Wang* 20262 (NY); *Men tou-kou, T. F. King* 2 (NY); *Ling-shan, T. F. King* 626 (A, NY); *Paefeng-tzi, C. W. Wang* 60802 (A); (*Tche-Ly*) *mont du Kouying, L. Chanet* 416 (HOLOTYPE of *Deutzia chanetii* Lévl., A); *Hsiao-wu-tai shan, J. Hers* 1476 (A), 2183 (A), 2185 (A); same locality, *J. C. Liu* 1889 (NY); *F. M. Meyer* 1304 (A); *H. Smith* 313 (A); *C. W. Wang* 6165 (A); *T. P. Wang* 482 (NY); without precise locality, *L. Chanet* 61 (A). *Shansi*: *Wu-tai shan, J. Hers* 2642 (A); *Ja siu, C. T. Ren* ex Univ. of Nanking Herb. no. 6123 (A); *Mien shan, R. W. Chaney* 1069 (NY). *Szechuan*: *Teng-hsiang-ying, H. Smith* 186 (A), 1935 (A).

CULTIVATED: *Europe*: Hort. Bot. Berol., *E. Koehne* 1904, 466 (A); Hort. Vilmorin; *Plantière C. Schneider* 1906. *United States*: *Arnold Arboretum* field no. 1769 (seed received from *Bretschneider*, flowered June 28, 1888); no. 1223 (introduced from *Vilmorin*, flowered in June 1899; no. 6596 (seed received from *W. Purdom*, Lot no. 174, flowered in June 1915), *S. Y. Hu*, June 1950. All this cultivated material has reddish brown nerves and petioles.

So far as I know the typical *P. pekinensis* Rupr. has been introduced to the western world on three occasions. Each introduction was in the form of seeds. The first came from *E. M. Simon*, who was collecting seeds in the hills west of Peking in 1862. These were sent to Paris in 1865. Plants raised from these seeds have reddish violet shoots, petioles, and nerves. *Carrière* in 1871 named the plant *P. rubicaulis*. The second introduction was by *Bretschneider*, who collected on the hills west of Peking in 1881-2. He sent the seeds to *C. S. Sargent* at the *Arnold Arboretum*, and also to *Kew* in England. Thus the living specimen now growing in the *Arnold Arboretum* is one of the oldest plants of this oriental species to be introduced into the western world. *William Purdom* collected seeds and specimens for the *Arnold Arboretum* in the mountainous area west and north of Peking, and his collections formed the third introduction of

this species. Plants raised from his seed, Lot no. 174, were first numbered Arnold Arboretum 6596, and later 20086. These plants first flowered in June 1915.

This species is a graceful compact shrub with the stems hidden by leafy branchlets. The current year's growth and the petioles are reddish brown. Just before the flowers open the buds have reddish purple stripes on the back. At anthesis the flowers are yellowish white with a pleasant fragrance. Many of the anthers bear no pollen. J. Hers recorded that in northern Shansi the people collect the young shoots and eat them as greens.

26a. *Philadelphus pekinensis* Rupr. f. *lanceolatus*, forma nov.

Frutex, ramulis glabris; foliis lanceolatis, 4–6.5 cm. longis, 1–2 cm. latis, basi cuneatis vel acutis, apice acuminatis, utrinque glabris, axilla nervorum barbatis; inflorescentiis 7-vel 9-floris, rhachibus 0.8–1.5 cm. longis, corolla subdisciformi, 2 cm. diametro.

CHINA: Hopei (Chihli): Hsiao-wu-tai-shan, C. F. Li 10522 (NY, TYPE).

This form differs from typical *P. pekinensis* Rupr. in having lanceolate leaves. According to the field label the type material was collected in August. It was in full bloom. Thus it is the latest blooming form known to the Old World.

27. *Philadelphus brachybotrys* Koehne ex Vilmorin & Bois, Frut. Vilm. Cat. Prim. 128. 1904. — Koehne in Sargent, Pl. Wils. 1: 5. 1911. — Bean, Trees Shrubs ed. 7, 2: 417. 1950.

*Philadelphus pekinensis* Rupr. var. *brachybotrys* Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 193, 1949.

TYPE: *M. L. de Vilmorin* (Herb. E. Koehne).

A large shrub up to 3 m. high, the bark of the second year's growth brownish gray, close; the current year's growth villose, becoming glabrescent. Leaves ovate, 2–6 cm. long, 1–3 cm. wide, rounded or obtuse at the base, shortly acuminate or acute at the apex, finely serrate or subentire, sparsely strigose above, strigose on the nerves beneath. Inflorescences 5- or 7-flowered, the lower pair of flowers often in the axils of normal leaves, the rachis 2–4 cm. long, sparsely villose, pedicels 3–5 mm. long, sparsely strigose, becoming glabrescent, hypanthium and calyx glabrous; sepals ovate, 4–6 mm. long, 3–4 mm. wide, acuminate; corolla cream-white, disciform, 2.5–3.5 cm. across, the petals suborbicular 1–1.5 cm. long, 1–1.3 cm. wide; stamens 31–40, the longest 8 mm. long; disc and style glabrous, the style subequal to the long stamens, the apical one third divided, the stigma spatulate, the abaxial surface 1 mm. long, the adaxial twice as long, narrowed gradually. Capsules ellipsoid, 7–10 mm. long, 5–7 mm. in diameter, the persistent calyx supermedian. Seeds short-tailed, the embryo 1–5 mm. long, the tail equaling the embryo in length.

CHINA: Kiangsu: Nanking, Ox-head mountains, in woods, *C. L. Tso* 991 (A).

CULTIVATED: Arnold Arboretum no. 6596 (plant from Hort. Vilmorin, 1901), *A. Rehder*, June 18, 1908 (A); Hort. C. S. Sargent (Vilmorin), *A. Rehder*, June 26, 1909 (A); (Pl. L. Späth, Berlin), *A. Rehder* 104 (A).

This species can be distinguished by its pubescent current year's growth, close brownish gray bark of the two-year-old branchlets, sparsely strigose leaves, short rather crowded inflorescence and suborbicular petals. It was first established on the basis of a plant cultivated in the garden of M. L. de Vilmorin in France. According to the records supplied to Koehne by Vilmorin, it was raised from seed sent to him by a Father Mouton from Tschen-Kéu, Kiangsi Province. I have not been able to learn anything about this French missionary, nor could I find any place in Kiangsi that sounded like Tschen-Kéu. Thus it is impossible for me to supply the exact place of origin of this species in China. *C. L. Tso* 991 from Kiangsu is the only spontaneous material which fits Koehne's description for this species and matches the specimen collected from plants sent us from Hort. Vilmorin. It is closely related to *P. pekinensis* Rupr., a glabrous species of the North China highlands.

27a. *Philadelphus brachybotrys* Koehne var. *laxiflorus* (Cheng), comb. nov.

*Philadelphus pekinensis* Rupr. var. *laxiflorus* Cheng in Contr. Biol. Lab. Sci. Soc. China 10: 113. 1936.

LECTOTYPE: *T. Tang & W. Y. Hsia* 383 (A).

Shrub up to 6 m. high, the second year's growth grayish brown or castaneous, closed, the current year's growth glabrous; leaves ovate, 4–9 cm. long, 2–4.5 cm. wide, obtuse, acute or on sterile shoots rounded at the base, acuminate at the apex, the acumen 5–10 mm. long, serrate, sparsely strigose or glabrescent above, strigose on the principal nerves beneath; racemes loose, 5-, 7-, 9-flowered, the rachis 4–8 cm. long, glabrous, pedicels 5–8 mm. long, after fruiting up to 11 mm. long.

CHINA: Chekiang: Tien-mo shan, *T. Tang & W. Y. Hsia* 383 (A, LECTOTYPE); same mountain, *H. H. Hu* 1551 (A), 1653 (A); West Lake, *H. H. Hu* 1497 (A); Yun-huo, *S. Chen* 1526 (A); Yen-tang shan, *C. Y. Chiao* ex Herb. Univ. Nanking no. 14682 (A); Chen-chiong, 40 miles south of Sia-chu, *R. C. Ching* 1740 (NY). Anhwei: Whang shan, *R. C. Ching* 2923 (A), 3005 (A).

CULTIVATED: Nanking, First Agriculture School, *Chen* 2549 (A).

This variety appears to be common in the woods of the mountainous areas in Chekiang. Cheng cited 23 collections from ten different localities of that province. It is also common in southern Anhwei. In these provinces the plants occur in open thickets by rocky cliffs or shady woods at altitudes of 300 up to 1500 meters. The white fragrant flowers appear in June and the early part of July.



28. *Philadelphus laxiflorus* Rehder in Jour. Arnold Arb. 5: 152. 1924.

Shrub 2–3 m. high, the bark of two years' growth grayish brown or castaneous, exfoliating; current year's growth glabrous, fuscous. Leaves ovate-elliptic or elliptic, 3–8 cm. long, 1.5–3 cm. wide, on weak branches sometimes 2 cm. long, 0.8 cm. wide, acute, obtuse, or on vegetative branches rounded at the base, acuminate at the apex, the acumen 5–15 mm. long, finely serrate, uniformly setose above, the hairs compressed, sparsely villose on the principal nerves beneath, often bearded. Inflorescences 7-, 9-, or 11-flowered, the lower pairs of flowers in the axils of normal leaves, the rachis 6–12 cm. long, glabrous; pedicels 6–10 mm. long, glabrous; hypanthium and calyx glabrous; sepals ovate, 6 mm. long, 4 mm. wide, acuminate; corolla disciform, 2.5–3 cm. across, the petals suborbicular, 1.6 cm. in diameter; stamens 30–35, the longest 9 mm. long; disc and style glabrous, the style as long as the longest stamens, the upper one third divided, the stigma clavate, the abaxial surfaces 1.8 mm. long, the adaxial twice as long, narrowed gradually. Capsules ellipsoid, 8 mm. long, 6 mm. in diameter, the persistent sepals supermedian. Seeds short-tailed, the tails half as long as the embryo.

CHINA: Shansi: Fang-shan Hsien, Nan-yang Shan, *J. Hers* 2704 (A). Shensi: Tsingling, 60 km. south of Sian, *J. Hers* 2959 (A); Tai-pei Shan, *Wm. Purdom* 439 (TYPE, A). Kansu: Kwan Shan, *G. Fenzl*, May 22–29, 1935 (A). Hupei (Hupé): Monte Si-ho (On-tang Scian), *P. C. Silvestri* 3004 (A); without precise locality, *P. C. Silvestri* 4358a (A, photo & fragment), 4359 (fragment, A); 4360 (fragment, A); Poa-ken, *P. C. Silvestri* 4361 (A); Scian-kin, *P. C. Silvestri* 4363 (A).

CULTIVATED: United States: New York: Highland Park, *E. H. Costich*, June 7, 1916 (A). Massachusetts: Hort. C. S. *Sargent*, June 3, 1913 (A).

This species is distinguished by its exfoliating castaneous bark, uniformly setose leaves, loose inflorescences, glabrous pedicels, clavate stigma, ellipsoid fruit, and short-tailed seeds. Its glabrous hypanthium suggests close relationship with *P. pekinensis* Rupr. But the latter species has glabrous leaves, crowded inflorescences, and globose fruits. Both morphologically and geographically this species is intermediate between *P. pekinensis* Rupr. and *P. sericanthus* Koehne. The pubescence of its leaves resembles that of *P. sericanthus* Koehne, but Koehne's species has pubescent hypanthia. It is probably a natural hybrid of a northern species with some southern influence. It occurs in woods at altitudes of 1500–2000 meters in the Tsingling mountains, and its range extends northward along the Shansi and Kansu border, reaching the Lu-liang mountains. Its white flowers appear in June.

Silvestri's collections from the eastern end of the Tsingling Range have been named and distributed under some unpublished binomials of *Pampanini*.

Series 4. *Coronarii* (Koehne) Rehder

*Philadelphus* subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 4. *Coronarii* (Koehne) Rehder, *Man. Cult. Trees Shrubs* ed. 2, 269. 1940; et *Bibl. Cult. Trees Shrubs* 192. 1949.

*Philadelphus* sect. *Stenostigma* subsect. *Coronarii* Koehne in *Gartenfl.* 45: 451, 596. 1896.

TYPE SPECIES: *P. coronarius* Linn.

Upright arching or dwarf compact shrubs, the bark of the second year's growth exfoliate; leaves ovate, elliptic or lanceolate, serrate or subentire; inflorescences 5- up to 9-flowered, rarely ternate; hypanthia glabrous, rarely with a few crisp weak hairs; corolla varied, disciform or cruciform, many doubled; stamens 21-25; style divided; capsules turbinate; seed with medium-long tails.

This series covers all the European and Caucasian elements. Due to the long period of cultivation and through controlled hybridization of growers or accidental crosses of remote species brought into close association in gardens, many hybrids and garden varieties are now in existence.

## KEY TO THE SPECIES

- A. Leaves ovate or elliptic; petals glabrous at the apex.
    - B. Disc and style glabrous. . . . . 29. *P. coronarius*.
    - BB. Disc and style pubescent. . . . . 30. *P. caucasicus*.
  - AA. Leaves lanceolate; petals hirtellous at the apex; rim of the disc hirsute; style glabrous. . . . . 31. *P. salicifolius*.
29. *Philadelphus coronarius* Linn., *Sp. Pl.* 470. 1753. — Kniphof, *Bot. Orig. Herb. Viv.* 5: pl. [65]. 1758. — Miller, *Dict. Gard.* ed. 8, [834]. 1768. — Hoppe, *Ect. Pl. Ratisb.* pl. 522. 1790. — Schmidt, *Oest. Allgem. Baumzucht* 1: 57, *pl.* 59, 60. 1792. — Curtis, *Bot. Mag.* 11: *pl.* 391. 1797. — Sturm, *Deutschl. Fl.* 1 (1): *pl.* [37]. 1798. — Lamarck, *Ill. Planches Bot.* pl. 420. 1791. — Willd., *Sp. Pl.* 2: 947. 1800. — D.C., *Prodr.* 3: 205. 1828. — Schrader in *Linnaea* 12: 388. 1838. — Loudon, *Hort. Brit.* 196. 1832; et *Arb. Frut. Brit.* 2: 951. 1838. — G. Don, *Gen. Syst.* 2: 807, *fig.* 114. 1832. — Schnizlein, *Iconogr.* 4: *pl.* 264. 1843. — Maxim. in *Mém. Acad. Sci. St. Pétersb.* VII. 10 (16): 36 (*Rev. Hydrang. As. Or.*). 1867. — Le Maout & Decaisne, *Traité Gén. Bot.* 260. 1868. — Koch, *Dendrol.* 336. 1869. — Boiss., *Fl. Orient* 2: 814. 1872. — Lavallée, *Arb. Segrez. Enum.* 114. 1877. — Hoffmann, *Pflanzenatlas*, *pl.* 39, *fig.* 244. 1881. — Nicholson, *Ill. Dict. Gard.* 3: 95, *fig.* 105. 1886. — Engler, *Pflanzenf.* III. 2a: 70. 1890; ed. 2, 18a: 191. 1930. — Koehne, *Deutsche Dendr.* 182. 1893; in *Gartenfl.* 45: 618. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904 (13): 85. 1904. — Dippel, *Handb. Laubh.* 3: 335. 1893. — Nicholson in *Kew Hand-List* 1: 225. 1894; ed. 2, 373. 1902. — Fiori & Paol., *Ic. Fl. Ital.* 195, *fig.*

1890. 1895; et Fl. An. Ital. 1: 544. 1895. — Britt. & Brown, Ill. Fl. N. States Can. 2: 186. 1897; ed. 2, 232. 1913. — Rydb. in N. Am. Fl. 22: 164. 1905. — Merino, Fl. Descr. Ill. Gal. 1: 477. 1905. — Syereishtchikof, Ill. Fl. Mosc. 2: 220, fig. 1. 1907. — Pereira, Fl. Port. 284. 1913. — Bonnier, Fl. Compl. France Suisse Belg. 4: 40, pl. 194. 1921. — Hegi, Ill. Fl. Mittel.-Eur. IV. 2: 640, fig. 978. 1922. — Liu in Bull. Pek. Soc. Nat. Hist. 2 (3): 103. 1925. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949. — Chen, Ill. Man. Chin. Trees Shrubs 374, fig. 280. 1927. — Bean, Trees Shrubs, ed. 7, 2: 411, pl. 34. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

*Frutex coronarius* Clus., Hist. 1: 55. 1601.

*Syringa suaveolens* Moench, Meth. 678, 1794.

*Philadelphus salzmanni* Hort. ex Koch, Dendrol. 1: 338. 1869. *nom. nud.*, in syn.

*Philadelphus kochianus* Koehne, Deutsche Dendr. 183. 1893.

*Philadelphus triflorus* Hort. ex Nicholson in Kew Hand-List 1: 225. 1894, non Wall.

*Philadelphus coronarius* var. *vulgaris* Schrad. ex DC., Prodr. 3: 205. 1828. — Loudon, Arb. Frut. Brit. 2: 951. 1838.

*Philadelphus aromaticus* Hort. ex Steud. Nom. 611. 1840.

*Philadelphus coronarius* var. *genuinus* Maxim. in Mém. Acad. Sci. St. Pétersb. VII, 10 (16): 37 (Rev. Hydrang. As. Or.). 1867. — Franch. & Sav., Enum. Pl. Jap. 1: 56. 1873.

*Philadelphus deyrolleanus* Lavallée, Arb. Segrez. Enum. 116. 1877.

*Philadelphus kochianus* Koehne, Deutsche Dendr. 188. 1893.

*Philadelphus pallidus* Hayek ex Schneider, Ill. Handb. Laubh. 1: 373, fig. 237, x-z; 238, h-k. 1905. — Hayek, Fl. Steierm. 1: 725. 1909. — Hegi, Ill. Fl. Mittel.-Eur. IV. 2: 641. 1922. — Prodan, Fl. Determ. Descr. Pl. România 1: pl. 8, fig. 88. 1923. — Engler, Pflanzenf. ed. 2, 18a: 192. 1930. — Sata, Ill. Manch. Mong. Trees ed. 2, 127, fig. 90. 1943.

*Philadelphus zeyheri* var. *kochianus* (Koehne) Rehder in Jour. Arnold Arb. 1: 201. 1920; Man. Cult. Trees Shrubs 277. 1927; ed. 2, 272. 1940; et Bibl. Cult. Trees Shrubs 194. 1949.

TYPE: Linnaean Herbarium No. 634.1.

An upright, rather stiff shrub with some arching branches, the second year's growth moderately exfoliate, the current year's growth brown, sparsely pubescent or glabrescent. Leaves ovate, 4.5–9 cm. long, 2–4.5 cm. wide, subglabrous, pubescent on the primary nerves and nerve-angles beneath; subdentate with 6 to 11 teeth on each side, obtuse or acute at the base, 3- or 5-nerved, acuminate at the apex. Flowers fragrant, the inflorescence a determinate raceme, 5- to 9-flowered, more on vigorous twigs or less on weak ones, the last pair usually in the axils of normal leaves, sometimes cymose; hypanthia glabrous with few hairs at the base merging into the sparsely pubescent pedicel; at anthesis the pedicels 6–10 mm. long, in fruit 6–20 mm. long; sepals ovate, 4–5 mm. long, glabrous; corolla subdisciform, 2.5–3 cm. across, the petals oblong-obovate, 12–14 mm. long, 11 mm. wide, the apex rounded; stamens ca. 25; disc and style glabrous,

the adaxial stigmatic surface three times longer than the abaxial. Capsules turbinate, 6–8 mm. long, 5–6 mm. in diameter, the persistent calyx sub-apical. Seed spindle-shaped, 3 mm. long, 0.75 mm. wide, the testa brown, slightly striate, the slender tail as long as the minute embryo.

AUSTRIA: Wien, *Handel-Mazzetti* on June 16, 1935 (A).

CAUCASUS: Borjom, *C. S. Sargent*, July 19, 1903 (A); Kuban, *N. Busch & P. Klopoto*w, May 1907 (A).

CULTIVATED: Europe: Upsala, Linnaean Herb. 634.1 (photo of TYPE, A). Hort. Göttingen, *A. Rehder* 1612, 1614, 1635, 1641, 1670, 2230 (all at A); Hanover, Botanischer Garten der Forstakademie, *H. Zabel* in 1873 (A). Hort. Simon Louis, Plantière, *C. K. Schneider* in 1906 (A). United States: Arnold Arboretum 4785–1 (A).

*Philadelphus coronarius* Linn. is the type species of the genus. It is also the most widely cultivated and the best known species of the genus. Written accounts about it can be found in almost all languages existing in the northern hemisphere. The relatively large number of references cited above represent only a selection from the more important literature regarding it. It has been associated with man since time immemorial, and its nativity is now obscure. Thus botanists have no agreement regarding its origin. Modern horticulturists and taxonomists like Bean of Kew and Rehder of the Arnold Arboretum consider it a native of southern Europe, from Italy to the Caucasus. I have not been able to find any statement to this effect in the floras of these regions. As early as the sixteenth century Clusius observed its occurrence in Spain, Austria and Hungary, remarking at the time that it had never been found in a wild state in those countries. He thought that it might have been first cultivated in Belgium. When Linnaeus established the species he doubtfully assigned its origin to Verona. Schrader in 1838 gave a negative statement as to the possibility of its spontaneous occurrence in southern Germany and Bohemia and suggested that it had probably been introduced from the Orient, possibly from Japan. Boissier in his *Flora Orientalis* maintained that it was not truly spontaneous in the area covered. As to the countries of southern Europe, I have not been able to find in the published floras of Italy, Spain, or Portugal any statement about its spontaneous occurrence in those countries.

Morphologically this species has the seed character of the Japanese element, the leaf and style characters of the Amur River element. In spite of the relative geographical proximity, its relationship with the Himalayan element is rather remote.

In early botanical literature there are two elements ascribed to *P. coronarius*. One is the material typified by the specimen in the Linnaean herbarium, and the other is represented by the plate in Bot. Mag. 11: *pl.* 391. 1797. The leaves of the plant pictured in this plate have coarser teeth, acute sepals, and elliptic petals. It suggests *P. lewisii* Pursh rather than the Linnaean species.

Cultivation has apparently proved that *P. coronarius* Linn. is a heterogeneous species. Through special care growers have segregated and prop-



agated many garden varieties which appear completely different from the typical form. Some of these forms are compact and dwarf, while others are stiff and rather loose in habit. Nearly all of them have short, depauperate inflorescences. Some of them are shy to flower, and some others rarely flower — for example, Dippel observed a twenty-year-old dwarf form which had never flowered. Many have double flowers. Some of them have been treated as putative hybrid species by some authors and forms or varieties of *P. coronarius* Linn. by others. As none of them occurs in the wild state, they are treated as garden varieties here.

# KEY TO THE VARIETIES OF *P. coronarius*

- A. Leaves uniformly green.
    - B. Low compact shrubs up to 1 meter high.
      - C. Leaves opposite, 2 at each node.
        - D. Pedicels villose. . . . . a. var. *duplex*.
        - DD. Pedicels glabrous.
          - E. Flowers highly doubled, the petals pointed at the apex. . . . . b. var. *deutziaeflorus*.
          - EE. Flowers semi-doubled, the petals rounded at the apex. . . . . c. var. *dianthiflorus*.
      - CC. Leaves verticillate, 3 at each node. . . . . d. var. *cochleatus*.
    - BB. Tall shrubs over 2 m. high, the branchlets stiff and loose, rarely drooping; leaves ovate, ovate-elliptic, or elliptic.
      - C. Flowers simple. . . . . e. var. *zeyheri*.
      - CC. Flowers doubled. . . . . f. var. *primulaeflorus*.
  - AA. Leaves variegated. . . . . g. var. *variegatus*.
- 29a. *Philadelphus coronarius* Linn. var. *duplex* West., Univ. Bot. 1: 205. 1770. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2. 271. 1940. — Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.

*Philadelphus nanus* Mill., Gard. Dict. ed. 8, 34. 1768.

*Philadelphus coronarius* Linn. var. *nanus* Aiton, Hort. Kew. 2: 155. 1789. — DC., Prodr. 3: 205. 1828. — Schrader in Linnaea 12: 390. 1838. — Anon. in Gard. 40: 289. 1891. — Dippel, Handb. Laubh. 3: 337. 1893. — Voss, Vilmor. Blumengärt. 1: 290. 1894. — Bean, Trees Shrubs ed. 7, 2: 412. 1950.

*Philadelphus coronarius nanus* Granz Schmidt, Oester. Allg. Baumz. 1: 57, t. 60. 1792.

*Philadelphus coronarius* var. *flore plena* Loddiges ex Loudon, Arb. Brit. 2: 951. 1838. — Anon. in Garden 40: 289. 1891.

*Philadelphus coronarius* Linn. var. *pumilus* West., Univ. Bot. 205. 1770. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940. — Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.

*Philadelphus coronarius* Linn. forma *pumilus* (West.) Rehder, Bibl. Cult. Trees Shrubs 193. 1949.

LECTOTYPE: Kew, *G. Nicholson* 1307 (A).

Dwarf shrubs, the branchlets castaneous, the bark of the second year's growth exfoliating, the current year's growth villose, the hairs compressed,

the leaves oblong-elliptic, 3–5 cm. long, 1–2.5 cm. wide, inconspicuously villose on both surfaces, serrate, those on the virgin shoots broad ovate, 6–8 cm. long, 4–4.5 cm. wide, abruptly acuminate, coarse dentate, uniformly villose, the hairs  $\pm$  erect; flowers doubled, ternate or in depauperate 5-flowered, rarely 7-flowered racemes with the lower ones in the axils of normal leaves, the pedicels 2–3 mm. long, villose; the hypanthium and calyx glabrous or glabrescent; corolla 2.5 cm. across, the petals oblong, rounded at the apex.

ENGLAND: Kew, *G. Nicholson* 1307 (A), 2597 (A).

GERMANY: Hort. Göttingen, *A. Rehder* 1606 (A).

AUSTRIA: *Henric Braun*, May 15, 1907 (A); *Handel-Mazzetti*, June 16, 1935 (A).

UNITED STATES: Massachusetts: Cambridge Bot. Gard., June 3, 1880 (A); Arnold Arboretum field no. 2784 (A). California: Univ. of California Bot. Gard. no. 3434.

This variety probably originated in the gardens of England, where it has been known as *nanus*. Rehder, in his Manual of Cultivated Trees and Shrubs, recognized two varieties, *duplex* and *pumilus*, both of which have *nanus* as a synonym. Although he gave no reason for this separation, one judges, from the material he worked with, that he named the flowering specimen *duplex* and the non-flowering specimens *pumilus*. The British *nanus* is well known for its tardiness in flowering. Dippel recorded one case where the plant was twenty years old and had never flowered. I have examined both the flowering and the sterile specimens with a microscope to see if there may be a difference in the type of hairs present on the branchlets and leaves. I see no reason for keeping *duplex* and *pumilus* as distinct varieties. As *duplex* is the older varietal name, it should be the valid name for this variety. It can be recognized by its dwarf habit, pubescent branchlets and leaves, tardiness and paucity in flowering, double flowers with glabrous hypanthia and calyces, and its rounded petals.

- 29b. *Philadelphus coronarius* Linn. var. *deutziaeflorus* Hartwig, Ill. Gehölzb. 258. 1892. — Schelle in Beissner & al., Handb. Laubh.-Ben. 128. 1903. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940.

*Philadelphus coronarius* Linn. forma *deutziaeflorus* (Hartwig) Rehder in Jour. Arnold Arb. 1: 201. 1919; et Bibl. Cult. Trees Shrubs 193. 1949.

*Philadelphus coronarius* Linn. var. *multiflorus plenus* Rehder in Bailey, Cycl. Am. Hort. 3: 1298. 1901, *nom. nud.*

LECTOTYPE: Arnold Arboretum 5852, *A. Rehder*, June 23, 1920 (A).

A low compact shrub, the branchlets castaneous, the bark of the second year's growth exfoliating, the current year's growth glabrous, the newly growing vegetative shoots inconspicuously pilose; leaves ovate, 2–5 cm. long, 1.5–2.5 cm. wide, glabrous on both surfaces, occasionally inconspicuously pilose on the principal nerves, subentire or finely serrate at the

apical end, those on the vegetative shoots up to 9 cm. long, 6 cm. wide, glabrous except on the principal nerves and nerve-angles beneath; flowers doubled, in 3's, or in depauperate 5-flowered racemes, the pedicels glabrous, 7–10 mm. long; hypanthium and calyx glabrous; corolla 3 cm. across, the petals more or less pointed at the apex.

UNITED STATES: Arnold Arboretum 5852, without collector, June 21, 1916 (A); *A. Rehder*, June 23, 1920 (A, LECTOTYPE).

This variety probably originated in the Späth Nursery at Berlin.

- 29c. *Philadelphus coronarius* var. *dianthiflorus* Dippel, Handb. Laubh. 3: 337. 1893. — *Rehder* in *Bailey*, Cycl. Am. Hort. [3]: 1298. 1901. — *Bean*, Trees Shrubs 2: 133. 1914, ed. 7, 2: 412. 1950. et in *Chitt.*, Dict. Gard. 3: 1546. 1951.

LECTOTYPE: Arnold Arboretum 2222-1, *A. Rehder*, June 23, 1920 (A).

A dwarf shrub with arching branchlets, the second year's growth gray, with close but tardily wearing off bark, the current year's growth glabrescent; leaves oblong-ovate, very weakly denticulate, 1.5–5.5 cm. long, 1–3.5 cm. wide, obtuse or rounded at the base, short and abruptly acuminate at the apex, glabrescent on both surfaces, those on the vegetative shoots up to 9 cm. long, 6 cm. wide, sparsely strigose-villose beneath; flowers in 3's, solitary or 5 in short determinate racemes, the pedicels, hypanthia and calyces glabrous; the corolla semidoubled, the petals rounded at the apex.

GERMANY: Botanischer Garten der Forstakademie, Hannover, *H. Zabel*, June 13, 1894.

UNITED STATES: Arnold Arboretum, *A. Rehder*, June 23, 1920.

This variety appeared first in German literature. It probably originated in that country. The above-cited *Zabel* collection represents the oldest specimen of this form that I have examined. This specimen records that as early as 1889 it was ready for distribution in the Späth nursery at Berlin. It is closely related to *P. coronarius* var. *primulaeflorus*. It can be readily distinguished from the latter variety by its dwarf habit, semidouble flowers, and glabrous pedicels. It is also closely related to *P. coronarius* var. *deutziaeflorus*. The latter variety has highly doubled flowers with pointed petals and more sharply serrate leaves.

- 29d. *Philadelphus coronarius* Linn. var. *cochleatus* Lavallée, Arb. Segrez. Enum. 114. 1877, *nom. nud.*

LECTOTYPE: *C. Schneider*, Sept. 1903 (A).

A low shrub, the branchlets glabrous, leaves 3 at a node, verticillate, broad-elliptic, 2–2.5 cm. long, 1–2 cm. wide, obtuse at both ends, subentire, with 2 or 3 minute, inconspicuous teeth on each side, glabrescent above, hirsute on the principal nerves beneath. The flowers not known.

FRANCE: Plantières, Herb. Dendr. Schneider, Sept. 1903 (A).

I have not been able to locate the valid publication of this trinomial. It apparently originated in France and has not been popular among growers. The only specimen that I have seen is sterile. The lower three pairs of leaves of this specimen are opposite, and the upper ones are verticillate, three at each node. Although there is no flower, I do not doubt its identity as a *Philadelphus*, and I think it is a distinct variety.

- 29e. *Philadelphus coronarius* var. *zeyheri* (Schrader) Hartwig & Rümpler, Baume Sträuch 391. 1875.

*Philadelphus zeyheri* Schrader ex DC., Prodr. 3: 205. 1828; et in Linnaea 12: 390. 1838. — Loudon, Arb. Frut. Brit. 2: 952. 1838. — Lavallée, Arb. Segrez. Enum. 115. 1877. — Rehder, Man. Cult. Trees Shrubs 277. 1927, ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 191. 1949. — Bean, Trees Shrubs ed. 7, 2: 420. 1950; et in Chitt., Dict. Gard. 3: 1547. 1951.

TYPE: Cultivated, *Schrader*, 1827 (Genève).

An erect shrub up to 2 m. high, the bark of the second year's growth castaneous, exfoliate, the current year's growth sparsely pilose; leaves ovate, those on the vegetative shoot 6–10 cm. long, 3–6 cm. wide, those on the flowering shoot 4–5 cm. long, 2.5–3.5 cm. wide, rounded or obtuse at the base, acuminate at the apex, serrate, glabrous above, sparsely pilose on the nerves beneath; inflorescences 3- or 5-flowered; when 5, the lower pair in the axils of normal or diminuted and lanceolate leaves; hypanthia glabrous; sepals ovate, 5 mm. long, 3 mm. wide at the base; corolla disciform, 2.5–3 cm. across, the petals suborbicular, 1–1.5 cm. in diameter; stamens ca. 32; disc and style glabrous, the stigma clavate, the adaxial surfaces 4–6 times longer than the abaxial; capsules turbinate, 7 cm. long, 6 cm. in diameter.

CULTIVATED: Europe: Kew, *G. Nicholson* 1318 (A), 1319 (A); Conservatoire et Jardin botaniques, *Schrader*, 1827 (Genève, TYPE; photo A); Bot. Gart. Forstakademie, Hannover 6, *H. Zabel*, June 17, 1873 (A), Sept. 1, 1873 (A); Wien, *N. Braun* in 1907 (A). United States: Arnold Arboretum 5881–1 = 15425, without collector, June 30, 1913 (A), Sept. 10, 1913 (A), June 13, 1914 (A); 7872, *A. Rehder*, July 18, 1918 (A), June 19, 1919 (A).

When *Schrader* published *P. zeyheri* he accredited the taxon to American origin. As its wild equivalent is not known in the New World, and as its exfoliation of the bark and dentation of the leaves match best with *P. coronarius* Linn., it is thus treated as a cultivar of this species. Rehder treated it as a putative hybrid between *P. coronarius* and *P. inodorus* or *P. grandiflorus*. Part of his material has pubescent discs. When those specimens are taken out, the rest fit well as a variety of *P. coronarius* Linn. What Rehder considered as  $\times$  *P. zeyheri* var. *kochianus* is a normal *P. coronarius* Linn.

- 29f. *Philadelphus coronarius* [var.] *primulaeflorus* [Carr.] T. Moore in Flor. Pom. 1873: 182, fig. 1873. — Rehder, Man. Cult. Trees



Shrubs 277. 1927; ed. 2, 271. 1940. — Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.

*Philadelphus primulaeflorus* Carr. Rev. Hort. 1870: 305, fig. 47. 1871. — Anon. in Gard. Chron. 1871: 5. 1871. — T. Moore, l.c.

*Philadelphus coronarius* forma *primulaeflorus* Nicholson, Ill. Dict. Gard. 3: 94, fig. 106. 1887. — Schelle in Beissner & al., Handb. Laubh.-Ben. 128. 1903. — Rehder, Bibl. Cult. Trees Shrubs 193. 1949.

*Philadelphus coronarius* var. *primulaeflorus plenus* Hartwig, Ill. Gehölzb. 258. 1892.

*Philadelphus coronarius* var. *rosaeiflorus plenus* Hort. ex Hartwig, l.c. — Moore in Bailey, Stand. Cycl. Hort. 5: 258. 1916, in syn.

*Philadelphus keteleeri* Hort. ex Dippel, Handb. Laubh. 3: 337. 1893, in syn.

*Philadelphus coronarius* var. *multiflorus plenus* Hort. ex Rehder in Bailey, Cycl. Am. Hort. [3]: 1298. 1901, *nom. nud.* — Moore in Bailey, Stand. Cycl. Hort. 5: 2580. 1916.

*Philadelphus coronarius* var. *plenus* Bean, Trees Shrubs ed. 7, 2: 412. 1950.

LECTOTYPE: Arnold Arboretum 6600, *A. Rehder*, June 19, 1919.

A compact tall shrub up to 2 m. high, with arching branchlets, the second year's growth castaneous, the bark exfoliating, the current year's growth sparsely but verrucosely villose, the hairs with thickened bases; leaves broad-ovate, 3–7 cm. long, 2–4 cm. wide, those on the vegetative shoots up to 9 cm. long, 7 cm. wide, rounded at the base, abruptly short-acuminate at the apex, sparsely pilose along the nerves above, strigose-villose beneath; flowers in 2's or 3's, solitary, or five in a crowded determinate raceme with the lower pair in the axils of normal leaves, the pedicels 4–8 mm. long, sparsely but uniformly villose, the hairs erect,  $\pm$  compressed; hypanthium glabrous, with a few hairs at the base or on the angles; calyx glabrous, broad-ovate, 6 mm. long, 3–4.5 mm. wide, acuminate at the apex; corolla 3–3.5 cm. across, with doubled petals; stamens generally sterile, with various modifications. Fruit obconic; seeds generally not fertile, with relatively short tails.

CULTIVATED: United States: Arnold Arboretum: *A. Rehder*, July 18, 1918 (A), June 19, 1919 (A); *E. J. Palmer*, June 11, 1936 (A).

This variety is of garden origin. Obviously it is a hybrid with unknown pedigree. Carrière, who first observed it in a French garden, interpreted it as a species. He did not give its history or establish its affinity. Two years later T. Moore summarized Carrière's account in English and reproduced the original illustration under the name *P. coronarius primulaeflorus*. He failed to give a definite rank to this trinomial, which I interpret as a variety. The subentire broad-ovate leaves and the relatively small number of flowers in each inflorescence, and the large sepals, suggest some relation with *P. inodorus* Linn. Based on obvious morphological characters, it is legitimate to assume it to be a hybrid between *P. coronarius* Linn. and *P. inodorus* Linn. According to available records this variety was introduced in America through the Arnold Arboretum in November 1908, under the field number 6600. The Späth Nursery in Berlin was then its distributor.

- 29g. *Philadelphus coronarius* Linn. var. *variegatus* Weston, Univ. Bot. 1: 205. 1770. — Lodd., Cat. 25. 1823. — Loudon, Arb. Frut. Brit. 2: 951. 1838. — Anon. in Garden 40: 209. 1891. — Chen, Ill. Man. Chin. Trees Shrubs 375. 1937. — Bean, Trees Shrubs 2: 134. 1914; ed. 7, 412. 1950.

*Philadelphus coloratus* Dippel, Handb. Laubh. 3: 338. 1893, pro parte.

*Philadelphus coronarius* forma *variegatus* (West.) Schelle in Beissner & al., Handb. Laubh.-Ben. 128. 1903. — Rehder, Cult. Trees Shrubs ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949.

*Philadelphus coronarius* Linn. fol. *argenteo-marginatis* Hort. ex Dippel. l.c., in syn. — Moore in Bailey, Stand. Cycl. Hort. 5: 2580. 1916.

LECTOTYPE: Hort. Parkman, June 19, 1881 (A).

A sickly-looking dwarf shrub, the second year's growth gray, the bark closed, tardily wearing off, the current year's growth sparsely villose; leaves ovate,  $\pm$  deformed, 2–3 cm. long, 1.5–2 cm. wide, white at the margin, rounded at the base, acute at the apex, glabrous or glabrescent above, sparsely villose, especially on the nerves beneath; flowers in 3- or 5-flowered depauperate racemes, the pedicels 2–6 mm. long, villose; hypanthium and calyx glabrous or glabrescent; corolla disciform, 2.5 cm. across, the petals suborbicular, 10 mm. in diameter; stamens ca. 25, many anthers appearing sterile; disc and style glabrous, the style 5 mm. long, divided almost to the base.

CULTIVATED: United States: Hort. Parkman, June 19, 1881 (A).

This variety was known to growers in England as early as 1770. There is no record about its origin. It is very likely a sport of *P. coronarius*. Although the standard manuals or encyclopedias of American horticulture all devote a line to this plant, it is extremely rare in American gardens. The above cited specimen is the only one that I have seen.

30. *Philadelphus caucasicus* Koehne in Gartenfl. 45: 619. 1896; et in Mitt. Deutsche Dendr. Ges. 1904 (13): 85. 1904. — Schneider, Ill. Handb. Laubh. 1: 374. 1905. — Poiarkova in Komarov, Fl. URSS 9: 220. 1939.

TYPE MATERIAL: Abchasien, *Karpinsky*; Kuban, *Kusnetsoff*; Pontische Region, *Kusnetsoff*.

An upright shrub with some arching branches, the second year's branchlets light brown, exfoliate, the current year's growth brown, weakly villose. Leaves elliptic or ovate-elliptic, 5–9 cm. long, 2–3, rarely up to 4 cm. wide, obtuse or acute at the base, 5- rarely 3-nerved, abruptly short-acuminate at the apex, subentire or very faintly and remotely serrulate, each side with 0 to 8 teeth, glabrous or glabrescent above, uniformly pubescent beneath, the hair villose. Flowers in determinate racemes, 5- to 9-flowered, the pedicels 3–10 mm. long, weakly villose; hypanthium and calyx weakly loose villose, the hair slightly crisp; sepals ovate, 5–6 mm. long, 3.5 mm. wide; corolla subdisciform, 3 cm. across, the petals obovate, 1.3 cm. long.

1 cm. wide, stamens ca. 22, the longest 6 mm. long, disk and style densely yellow villose, the style 6 mm. long, the upper one-third divided, the stigma clavate, the adaxial surface on a narrow ridge, twice as long as the abaxial. Capsules turbinate, 6–7 mm. long, 5–8 mm. across the top, the persistent sepals apical. Seed rather plump, short-caudate, the embryo ca. 1.25 mm. long, 0.75 mm. wide, the tail half as long as the embryo, often obtuse, the crown with rounded lobes.

EUROPE: Russia: Kutais, *A. Lomoikin*, May 1922 (A). Transcaucasia: Azerbajdzhan, distr. Zakataly, *I. Beidemann*, July 21, 1935 (A).

Koehne proposed this species on the basis of three collections, not designating any one as the type. As these materials are not available to me, the identification of this species is made on the basis of his description. Accordingly, the specimens with uniformly pubescent lower leaf-surfaces, weakly pubescent hypanthia and sepals, and pubescent disc and style are interpreted as the typical *P. caucasicus* Koehne.

The Caucasian material that I have examined demonstrates an obvious difference in the density of the hairs on the hypanthia and styles. Some plants apparently have glabrous hypanthia and styles. The fruiting specimens of these plants also have glabrous lower leaf-surfaces. In this respect they approach *P. coronarius* Linn. Nevertheless they can be distinguished from the latter species by their pubescent discs. The plants cultivated in outstanding American botanical gardens are this glabrous form. That in the Arnold Arboretum, numbered 21326-B, exhibits variations in the sizes of the leaves and flowers. On a vigorously growing branchlet the leaves are 6 cm. long and 3 cm. wide, and the petals are 12 mm. wide. On a weak branchlet of the same plant the leaves are only 3 cm. long, 1.3 cm. wide, and the petals are 8 mm. wide. The indumentum on the large and small leaves and flowers is the same. This observation seems to prove that the pattern of the indumentum of the individual plants in this group is a rather stable character. Thus I think the glabrous form is distinct enough to warrant a varietal name.

There is a yellow-leaved old garden form which has been assigned as a variety of *P. coronarius* in standard manuals dealing with trees and shrubs for the last half-century. An examination of the specimens at hand, sent to the Arnold Arboretum from various botanical gardens, reveals that they all have pubescent styles and discs. Thus a transfer is necessary.

#### KEY TO THE VARIETIES OF *P. caucasicus*

- A. Tall mound-shaped shrub up to 2.5 m. high; leaves green; hypanthia very sparsely pilose or glabrous. . . . . a. var. *glabratus*.
- AA. Low shrub 1–1.5 m. high; leaves yellow; hypanthia uniformly sparsely villose. . . . . b. var. *aureus*.

30a. *Philadelphus caucasicus* var. *glabratus*, var. nov.

*Philadelphus caucasicus* sensu Rehder, Man. Cult. Trees Shrubs ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949, non Koehne.

Frutex 2–2.5 m. altus, ramis griseis, bienniis castaneis, exfoliatis, hor-notinis sparse villosis; foliis ellipticis vel ovato-ellipticis, 3–7 cm. longis, 1.5–3 cm. (raro usque ad 4 cm.) latis, basi acutis, obtusis, raro rotundatis, apice breviter acuminatis, supra glabris vel glabrescentibus, raro sparse strigoso-villosis; inflorescentiis racemosis, 7- usque ad 11-floribus; pedicellis, hypanthiis et calycibus glabris, disco villosus, stylo glabro.

EUROPE: Caucasus: Tiflis, *S. Michajlowsky*, Sept. 1903 (A); Kutais, *A. Lomoikin*, May 1922 (A); Kuban, *V. J. Vorobjew & B. N. Klopoto*, July 1, 1906 (A, TYPE); same locality, *N. Busch & B. Klopoto*, May 11, 1907 (A).

CULTIVATED: Europe: Hort. Göttingen, *A. Rehder* 1609 (A), 1637 (A); Hort. Müskau, *A. Rehder*, July 1888 (A); Bot. Gart. Forstakademie 15, *H. Zabel*, June 17, 1873 (A). United States: Arnold Arboretum 6964, without collector, June 13, 1914 (A); 21703–A, *E. J. Palmer*, June 6, 1936 (A); 21703–B, *E. J. Palmer*, June 18, 1940 (A), *S. Y. Hu*, June 8, 1951 (A); 22482, *E. J. Palmer*, June 10, 1927 (A); 948–27, *C. E. Kobuski & C. K. Allen* in 1933 (A).

The genuine *P. caucasicus* Koehne has not been known in cultivation. The plants introduced into American gardens from the Caucasus belong to this variety. Arnold Arboretum 21707–A is raised from seed obtained from the Botanical Garden at Tiflis, and 21326–B came from the Boyce Thompson Institute, Yonkers, N. Y.

### 30b. *Philadelphus caucasicus* var. *aureus* (Rehder), comb. nov.

*Philadelphus coronarius* var. *aureus* Hort. ex Rehder in Bailey, Cycl. Am. Hort. [3]: 1298. 1901.

*Philadelphus coronarius* var. *fol. aureis* Hartwig, Ill. Gehölzb. 259. 1892.

*Philadelphus coronarius* forma *aureus* Hort. ex Schelle in Beissner et al., Handb. Laubh.-Ben. 128. 1903.

LECTOTYPE: Arnold Arboretum 5953, without collector, June 11, 1914 (A).

A sickly-looking shrub, 1.5 m. tall, the bark of the second year's growth castaneous, exfoliating, the current year's growth sparsely villose; leaves ovate, 3–5 cm. long, 1.5–3 cm. wide, obtuse or rounded at the base, shortly acuminate at the apex, yellow-green, prominently serrate, glabrous above, strigose-pilose on the principal nerves and in their angles; inflorescences 5-, 7-, rarely 3- or 9-flowered, the hypanthia with few hairs at the base, the sepals glabrous, ovate, 5 mm. long, 3–4 mm. wide; corolla disciform, 2.5 cm. across, the petals oblong-suborbicular, 11 mm. long, 10 mm. wide, the apex rounded; stamens ca. 22; disc hirtellous, style glabrous, the stigma clavate.

CULTIVATED: Europe: Kew, *G. Nicholson* 1006 (A); Breslau, Scheitniger Park, *C. Baenitz*, June 20, 1905 (A). United States: Arnold Arboretum 5953, without collector, June 11, 1914 (A, LECTOTYPE).

This is a rare variety. I have seen it only once, on Rockview Street, Jamaica Plain, Mass.



31. *Philadelphus salicifolius* Koch, Dendr. 1: 337. 1869.

*Philadelphus coronarius* var. *salicifolius* (Koch) Jäger, Ziergeh. ed. 2, 236. 1884.  
 — Dippel, Handb. Laubh. 3: 337. 1893. — Schneider, Ill. Handb. Laubh.  
 1: 374. 1905. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271.  
 1940. — Chen, Ill. Man. Chin. Trees Shrubs 375. 1937. — Bean, Trees  
 Shrubs ed. 7, 2: 412. 1950.

*Philadelphus coronarius* forma *salicifolius* (Koch) Voss, Vilmor. Blumengärt.  
 1: 290. 1894. — Rehder, Bibl. Cult. Trees Shrubs 193. 1949.

LECTOTYPE: Arnold Arboretum 18070, S. Y. Hu, June 14, 1951 (A).

A dwarf compact shrub up to 1 m. high, the second year's growth castaneous, the bark exfoliate, the current year's growth glabrous or glabrescent. Leaves lanceolate, those on the flowering shoot 3.5–7 cm. long, 1–1.5 cm. wide, acuminate at both ends, glabrous on both surfaces, rarely with few weak hairs on the principal nerves beneath, remotely and inconspicuously serrulate, those on the vegetative shoots 8–13 cm. long, 2–3 cm. wide, occasionally ovate on abnormal off-shoots, 7–8 cm. long, 5–6 cm. wide, acute or rounded at the base, acuminate at the apex. Flowers ternate, solitary or on depauperate racemes, the pedicels 2–4 mm. long, glabrous or sparsely villose, the hypanthium and calyx glabrous; sepals ovate-lanceolate, 5–6 mm. long, 2 mm. wide at the base; corolla stellate, 2–3 cm. across, the petals oblong-lanceolate, 1.2–1.4 mm. long, 5 mm. wide, the apex acutish, hirtellous; stamens ca. 21, the rim of the disc pubescent, style 5 mm. long, glabrous, divided almost to the base, the stigmas clavate, the abaxial surface half as long as the adaxial.

CULTIVATED: Europe: Bot. Gart. Forstakademie, Hannover, H. Zabel 27 (A); Hort. Bot. Leipzig, C. K. Schneider, June 26, 1904 (A); Hort. Simon Louis, Plantières, C. K. Schneider, June 25, 1906 (A). United States: Arnold Arboretum field no. 5875, E. J. Palmer, May 11, 1936 (A); without collector, June 21, 1916 (A); 18070, June 21, 1927 (A); S. Y. Hu, June 14, 1951 (A, LECTOTYPE).

This distinctive taxon probably originated in Germany. Koch recorded its existence as early as 1869. In the last three quarters of a century, botanists and horticulturists were inclined to interpret it as a variety or a form of *P. coronarius* Linn. This is probably due to the fact that suckers with broad-ovate *coronarius*-type of leaves often shoot from a normal dwarf *salicifolius* plant. Nevertheless, the distinctiveness of this taxon does not lie in its leaf-form. Its depauperate inflorescences, stellate corolla, oblong-lanceolate petals hirtellous at the apex, its small number of stamens, its much divided style, and its pubescent disc are of sufficient distinction to warrant specific rank. Its relationship seems to be closer to *P. caucasicus* Koehne than to *P. coronarius* Linn. Although this species has been known for almost a century, its distribution is very limited. So far as I know it exists only in a few botanical gardens. This lack of popularity among growers is probably due to its shy-flowering nature. It came to America in 1908 through the Arnold Arboretum, where it has been propagated by cuttings. Späth Nursery at Berlin, if not the originator, has been the chief distributor of this species.

(To be continued)

INDUCTION OF EARLY FLOWERING OF ORNAMENTAL  
APPLE TREES

KARL SAX AND ALBERT G. JOHNSON

HORTICULTURISTS have long known that the time of flowering of fruit trees could be hastened by various treatments which inhibit vegetative growth. The blocking of phloem transport from the leaves to the root system has been effected by girdling the trunk of the tree, by grafting on dwarfing rootstocks, or, more recently, by inverting a ring of bark on the trunk of the tree (6). Root pruning or confining the root system in pots also inhibits vegetative growth and promotes flowering. Pot binding has long been used to produce dwarf ornamental trees in Japan, and European foresters have used root pruning to promote early seed production in tree-breeding experiments. The bending of branches in a horizontal position also promotes early fruiting and is the basis for the "Spindlebush" method of training fruit trees in Europe.

The general relationship between growth of trees and the production of flowers and fruits was described by Thomas Andrew Knight (2) as follows: "According to that hypothesis, the true sap of trees is wholly generated in their leaves, from which it descends through their bark to the extremities of their roots, depositing in its course the matter which is successively added to the tree; whilst whatever portion of such sap is not thus expended sinks into the alburnum, and joins the ascending current, to which it communicates powers, not possessed by the recently absorbed fluid. When the course of descending current is intercepted, that necessarily stagnates, and accumulates above the decorticated space; whence it is repulsed, and carried upward, to be expended in an increased production of blossoms, and of fruit. . . . The repulsion of the descending fluid therefore accounts, I conceive satisfactorily, for the increased production of blossoms, and more rapid growth of the fruit upon the decorticated branch." Radioactive tracer tests and chemical analyses of the leaves of dwarfed trees done by graduate students at the Bussey Institution confirm Knight's observations made nearly 140 years ago.

The various methods for promoting earlier flowering and fruiting appear to be related to auxin formation and nutritional balance. The suppression of auxin production or accumulation associated with decreased vegetative growth is generally related to precocious flower and fruit production (1). Nutritional balance also appears to be involved in the production of flower buds. According to Klebs a high ratio of carbohydrates to nitrogen and mineral nutrients promotes flowering (3). This conclusion was supported by the later work of Kraus and Kraybill. More recently Roberts (4) found that flowering of shaded *Xanthium* plants could be hastened by spraying the leaves daily with a sugar solution. Although there is considerable evi-

dence in support of the control of flowering by the carbohydrate-nitrogen ratio, the relationship does not appear to be a simple one (1).

Precocious flowering of apple trees may also be promoted by the physiological incompatibility between the rootstock and the grafted scion variety. Certain rootstock varieties greatly inhibit the growth of the bud or scion of certain horticultural varieties of apples, but if the rootstock variety is used as an interstock on a compatible rootstock the dwarfing effect is greatly reduced. In these cases the dwarfing effect is not due to a poor graft union or to the checking of phloem transport through the dwarfing rootstock stem, but is caused by the interaction between the root system and the scion variety (5).

There is also some evidence that flowering may be induced by a "flowering hormone." This idea was first proposed by Sachs. In 1883 he found that cuttings taken from flowering begonias bloomed much earlier than cuttings taken from plants which had not bloomed. Vöchting grafted adventitious buds of beets into one- and two-year-old roots. The buds on the one-year-old roots produced only vegetative shoots, but those on two-year-old roots produced flowering stems. Cuttings or scions from old trees will usually flower earlier than those from immature trees (3). The grafting of scions from young seedlings on mature fruiting trees to hasten flowering and fruiting of the seedling variety may involve the transmission of a "flowering hormone" from stock to scion, since this method of inducing earlier flowering is not related to the suppression of vegetative growth. Similar evidence for the transmission of a flowering-inducing substance is found in grafts of certain herbaceous plants. Long-day non-flowering plants were induced to flower, even under the influence of long days, by grafting on them short-day variety scions bearing flower buds (1). Although no specific plant substance has been isolated which will stimulate flowering, there is considerable indirect evidence to support Sachs' theory that flowering may be induced by a specific hormone which is formed or accumulated by various internal and external factors.

Experiments with an apomictic variety of ornamental apple variety seem to support the concept of a "flowering hormone." The apple variety used was a hybrid between *Malus Sargentii* and *M. astracantha* designated by the planting number 33340. *Malus Sargentii* when open pollinated is completely apomictic and breeds true from seed. When artificially pollinated with pollen of certain species it does produce some sexual hybrids. The hybrid 33340, like the mother parent, is also apomictic and breeds true from seed. The original hybrid first flowered at the age of six years, and its apomictic seedlings produce flowers at about the same age. Since the hybrid is apomictic it is possible to test the fruiting response of old and young seedling trees which are of identical genetic constitution.

An attempt to induce early flowering by grafting scions from the young one-year-old seedlings on the original fruiting tree was only partially successful. Four grafts were made in 1951. One of the grafted scions flowered in 1953 and again in 1954, but the other three scions have not yet bloomed.

Scions from the fruiting mother tree were grafted on the apomictic seed-

lings in 1951. The two surviving grafts flowered sparsely in 1953 at the age of three years, but did not flower in 1954. The fact that a scion from a young apomictic seedling grafted on the mature mother tree and the scions from the fruiting tree grafted on the apomictic seedlings produced flowers in the third year, as compared with six years for the seedlings, does suggest the presence of a flowering stimulating substance in the fruiting tree.

More critical evidence was obtained by budding genetically uniform dwarfing rootstocks with buds from both the fruiting hybrid 33340 and its apomictic seedlings. The dwarfing stock used was Ottawa 524 budded on *Malus sikkimensis*, an apomictic species which has been found to be semi-dwarfing when used as a rootstock. In 1951 buds from the hybrid 33340 mother tree and from its apomictic seedlings were budded on uniform rootstocks of Ottawa 524/*M. sikkimensis*.

The resulting trees were grown in the nursery for a year and then transplanted to a test plot. They were spaced six feet apart in a single row, alternating the five "old bud" with the five "young bud" trees. In 1953 one of the "old bud" trees produced flowers and fruits, but no flowers were produced by any of the other trees. In 1954 all of the trees from the "old buds" produced flowers and fruits, while no flowers were produced on any of the trees propagated from buds of the young seedlings. The data regarding flowering, fruiting, and tree size are shown in TABLE 1.

TABLE 1

Performance of trees from buds from an old fruiting tree (O), and from buds of a young apomictic seedling (Y) from the old fruiting tree. Budded in 1951 on Ottawa 524/*Malus sikkimensis*.

Tree Number	Source of Bud	Flower Clusters		Fruit 1954	Trunk Caliper cm. June 1954
		1953	1954		
1.	O	0	15	43	2.2
2.	Y	0	0	0	2.3
3.	O	21	34	103	1.9
4.	Y	0	0	0	2.2
5.	O	0	24	75	2.2
6.	Y	0	0	0	2.3
7.	O	0	42	104	2.2
8.	Y	0	0	0	2.3
9.	O	0	14	54	2.1
10.	Y	0	0	0	2.0
Ave.	O	..	26	76	2.1
	Y	..	0	0	2.2

There is no evidence that the initiation of flowering in the "old bud" trees was caused by the suppression of vegetative growth. Tree number 3 from an "old bud" was smaller than the adjacent "young bud" trees (num-



bers 2 and 4), presumably because it had borne a relatively heavy crop of fruit for such a small tree in the previous year. The four other "old bud" trees, which did not fruit in 1953, were no smaller than the adjacent "young bud" trees. All trees of both lots were identical in morphological characters.

The abundant fruiting of the "old bud" trees in the third year of growth may be due in part to the dwarfing rootstocks, yet the "young bud" trees on the same clonal rootstocks produced no flowers or fruits at the same age. Scions from the fruiting mother tree grafted on 33340 seedlings did produce some flowers the third year, whereas the original hybrid and several of its apomictic seedling progeny did not flower until the sixth year. Although the number of trees tested is small, the consistent results do suggest the transmission of some substance which promotes flowering in the buds or scions from the fruiting tree.

If there is transmission of a flowering hormone or "florigen" through the buds from fruiting trees, one might expect the "florigen" to be transmitted through the apomictic seeds from the mother tree. However, the transmission by vegetative propagation, but not by seed, is not inconsistent with the behavior of the viruses which are transmitted by grafting but not by seed.

The induction of flowering and fruiting can be stimulated in many ways, — by pruning or confining the root system, by grafting onto dwarfing stocks, by ringing or inverting the bark on the trunk of the tree, by knotting the stem, by training the branches in a horizontal position, and in some plants by vernalization or by changing the photoperiod. Only in a few cases has the artificial addition of auxin proved effective in promoting flowering. It is also possible that anti-auxin may play a role in flower induction and that vegetative growth and flowering are controlled by a balance between auxin and anti-auxin, but there is as yet little evidence to support this theory (1).

It seems improbable that all of the various flower-inducing techniques act in the same way. For example, the inversion of a ring of bark on the trunk of a young apple tree undoubtedly inhibits the flow of nutrients to the root system. But the inversion of a ring of bark on one of many branches of a large apple tree also checks vegetative growth and promotes fruiting of the branch involved, but has little or no effect on the rest of the tree. The checking of phloem transport by various means does affect the nutritional balance of the tree, but this is probably only one of a number of factors in promoting flowering.

The apparent transmission of a flowering stimulus by buds from fruiting trees may not be related to the production of flowers and fruits by the tree from which the buds are taken. Differences in tree vigor, size of the leaf associated with the bud, and differences in nutritional balance may be causal factors in promoting earlier fruiting. In order to test some of these possibilities buds from vigorous one-year-old McIntosh whips and buds from mature bearing McIntosh trees were budded on clonal rootstocks in 1951. Eight of each type were planted in a test plot at the Arnold Arboretum's Case Estate in Weston, but none has yet produced flowers. Since

the young whips came from buds from a fruiting tree their buds might be expected to transmit the "flowering hormone," even though the whips would not reach the fruiting age for several years.

We have also selected buds in August from a branch which had a section of bark inverted in June, and at the same time taken buds from a normal branch of the same tree and put these buds on clonal rootstocks. The branch with the bark inversion should flower earlier than the normal branches, and we might expect buds from the bark inversion branch to produce earlier fruiting trees than those from the normal branch, even though neither branch had ever borne flowers or fruits. These and other experiments in progress should provide more information on the nature of early induction of flowering.

### SUMMARY

Buds from a fruiting apomictic ornamental apple tree and buds from its young seedlings were budded on uniform clonal dwarfing stocks in 1951. Of the five trees from the "old" buds, one flowered in 1953 and all flowered in 1954. None of the five trees from the "young" buds have yet produced any flowers. The earlier flowering of the trees from the "old" buds cannot be attributed to the suppression of vegetative growth. The evidence, although not conclusive, supports the assumption that a flower-stimulating substance was transmitted by the buds from the fruiting tree, but not by the apomictic seeds of the fruiting tree.

THE ARNOLD ARBORETUM AND  
THE CABOT FOUNDATION

### LITERATURE CITED

1. AUDUS, L. J., 1953. Plant growth substances. Interscience Publishers, Inc., New York.
2. KNIGHT, THOMAS ANDREW, 1820. Physiological observations upon the effect of partial decortication, or ringing the stems or branches of fruit trees. *Trans. Hort. Soc. London* 4: 159-162.
3. MAXIMOV, N. A., 1930. A textbook of plant physiology. McGraw-Hill Book Co., New York.
4. ROBERTS, R. H., 1951. Induction and blossoming of *Xanthium*. *Science* 113: 726-728.
5. SAX, KARL, 1953. Interstock effects in dwarfing fruit trees. *Amer. Soc. Hort. Sci.* 62: 201-204.
6. ———, 1954. The control of tree growth by phloem blocks. *Jour. Arnold Arb.* 35: 251-258.

## RHODODENDRON MACROPHYLLUM D. DON EX G. DON

LEONARD F. FRISBIE

THERE IS BUT ONE SPECIES of *Rhododendron* with persistent or ever-green leaves that is native to the west coast of North America. A measure of confusion arising from a number of causes has prevented unanimous agreement as to the correct name of this species. In an effort to clarify matters The Tacoma (Wash.) Rhododendron Society, Inc., carried out a research project bearing on this problem. Results of this research were published by the Society in *Rhododendrons* 4 (9): 2-4. 1954. The present note is an attempt to bring this study to the attention of a wider public.

A complete synonymy of the species is to be found in "Bibliography of Cultivated Trees and Shrubs," by Alfred Rehder, p. 505, published by the Arnold Arboretum of Harvard University, 1949. With an understanding in mind that the International Code of Nomenclature assigns validity to the name used in the first published description without exception, it seems a very simple matter to observe that *Rhododendron macrophyllum* D. Don (1834) has precedence over *Rhododendron californicum* Hooker (1855). In fact it is a simple matter if one looks no further than Rehder's synonymy. The later epithet is in error, but circumstances in England surrounding the two published descriptions prove to be interesting indications of the reasons why the mistake was made.

David Don wrote the first description, using herbarium material. His younger brother, G. Don, published it in his "General System of Gardening and Botany" 3: 843. 1834. The description follows:

"*R. macrophyllum* (D. Don, mss. in herb. Lamb.) leaves lanceolate, acute, glabrous on both surfaces as well as peduncles, rounded at base; ovarium bristly. Native of N. W. coast of America, where it was collected by Menzies. Petioles an inch long. Flowers copious, smaller than those of *R. maximum*, white. Calycine lobes short, rounded. Filaments glabrous. Long-leaved rhododendron. Shrub."

As will be noted, Don's description is rather incomplete and sketchy, and he considered the flowers to be white. Menzies makes no mention in his "Journal of Vancouver's Voyage" of having seen a white-flowered *Rhododendron*, and live material which he brought back to England proved to be pink-flowered. The designated color of the flowers in the description should have caused no confusion, but evidently it did. Dr. J. MacQueen Cowan of Scotland, who does the revision of *Rhododendron* classification for the Royal Horticultural Society, London, states that the color of the flowers of a *Rhododendron* species has no bearing on the validity of a first published description.

Don was evidently mistaken in stating that the filaments were glabrous. Field observations made in 1954 revealed that the filaments were pubescent

on the lower third in both the white-flowered and the pink-flowered forms.

Sir William Jackson Hooker did most of the work of describing and naming the plants which Menzies brought back from the northwest coast of North America, and his relation to the collection was semi-official. His description of the rhododendron was much more detailed than Don's. He worked from live material growing at Kew. Hooker published his description in the "Botanical Magazine," which has always had a place of great influence in British horticulture, and it was accompanied by a color drawing. These factors combined to give a very important place to Hooker's description when it was published in *Botanical Magazine* 81: *pl.* 4863. 1855. Hooker's description follows:

"*R. californicum*. Apparently a small or moderately sized shrub, with the habit of small plants of *Rhododendron maximum*, or still more of *Rhododendron catawbiense*, having stout branches, of which the younger ones are green and subherbaceous. Leaves on short petioles, three to four inches long, elliptical, obovate, acute, often almost mucronate at the point, tapering at the base, except in the upper leaves, glabrous and naked on both sides, paler colored on the under side. Beneath the flowers the leaves are generally more crowded, so as to form a sort of involucre to the large umbellate head. Calyx small, five lobed; the lobes form a broad base, almost subulate, slightly hairy. Corolla in bud rich carmine, when fully expanded broad campanulate; tube short suddenly spreading into five, broad, oval, crisped lobes; the ground color is then pale pink, deeper toward the apex of the lobes, and streaked with darker rose; thickened and downy below. Anthers deep pink. Ovary elliptical, with five longitudinal furrows, clothed with long, appressed silky hairs, five celled. Style rather larger than the stamens, glabrous. Stigma with five very minute points."

Hooker ignored Don's earlier description and his epithet was used in "Species of Rhododendron," published by the former British Rhododendron Association, and it has also appeared in successive editions of the "Rhododendron Handbook," now published by the Royal Horticultural Society. Rhododendron workers generally, including those of America, have followed these publications in the use of Hooker's epithet. The editor of Menzies' "Journal of Vancouver's Voyage," Dr. C. F. Newcombe, used *Rhododendron californicum*, marginal note, p. 20, the Preface XVIII, and also in the Appendix. The Washington state law designating this species as the State Flower makes the same error.

For some time, however, nearly all American scientists and botanists, and all herbaria, have correctly used *Rhododendron macrophyllum*. This is due in part to the influence of the published works of the late Alfred Rehder of the Arnold Arboretum.

All of the facts as stated above were presented to Dr. J. MacQueen Cowan and an appeal was made to him for a decision as to the correct epithet. He is positive that Don's *Rhododendron macrophyllum* has valid precedence, and that the use of *Rhododendron californicum* is in error. The Editors of the Royal Horticultural Society's publications in London have agreed to accept Don's epithet for use in future publications.



In the London publication, "Species of *Rhododendron*," p. 583, the statement is made: "*R. macrophyllum* is generally regarded as a form of this species with white and smaller flowers." Don stated in his description that the flowers were smaller than those of *R. maximum*. It is a mistake to infer that there is a difference in the size of the flowers of the two color forms. This same publication states: "HABITAT: California. On mountains at 1500 ft. altitude." This is an incomplete statement of the distribution of the species. The population in either Washington or Oregon is heavier than that of California. The species is known from southern British Columbia to Santa Cruz County, California. Populations in the coastal areas are exceedingly numerous.

While searching for exceptional forms of *Rhododendron occidentale* in Curry County, Oregon, in May 1954, field workers of the Tacoma (Wash.) *Rhododendron* Society, Inc., came upon a colony of seven plants of the extremely rare white-flowered form of this species (*R. macrophyllum*). The flowers were photographed and herbarium and propagating material was collected. An eighth member of the colony had been dislodged and left exposed to die by a logging bulldozer. Wood from the trunk of this plant was taken for an annular ring count. The diameter of the trunk was 3", and the age was 30 years. Details of this form are given below:

***Rhododendron macrophyllum* D. Don ex G. Don, f. *album* Rehder in Jour. Arnold Arb. 28: 254. 1947.**

HABIT: tall, growing to 30 ft., open, tree-like shrub sparsely branched.

LEAVES: elliptic to 18 cm. long, 7.5 cm. wide, cuneate at base, acute or mucronate at apex, glabrous on both surfaces, color lighter below.

INFLORESCENCE: 15 to 25 flowers, rachis ca. 1.5 cm. long.

COROLLA: pure white with dots on upper lobe, Sap Green HCC 62/1, clear color with no brown area as in type, 5 lobed, 5-6.5 cm. across, pedicel ca. 3.5 cm. long.

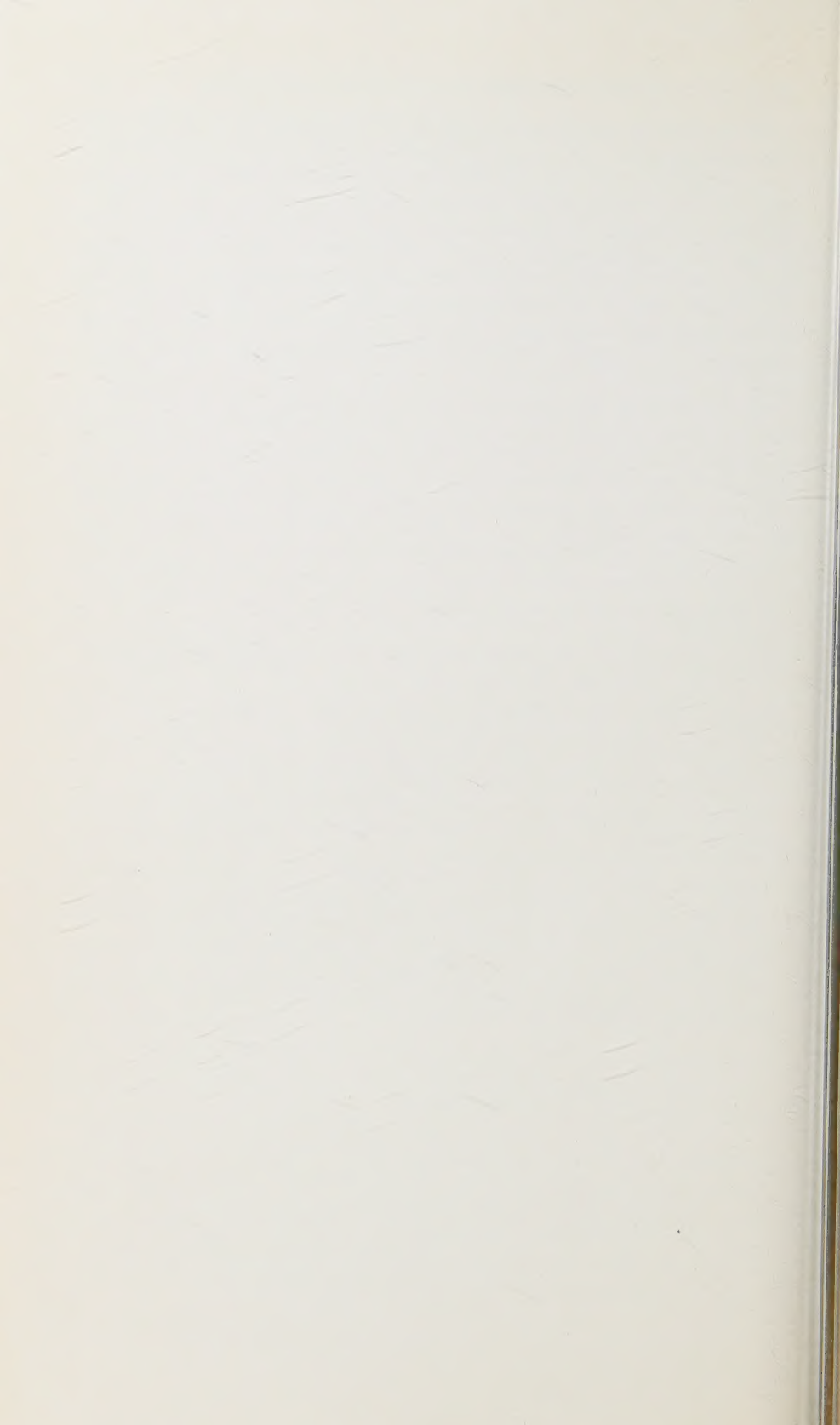
STAMENS: 10, 2-2.5 cm. long, pubescent below.

PISTIL: 3.75 cm. long, glabrous, ovary densely tomentose.

LOCALITY: northeast of Sixes, Curry County, Oregon, USA, on an abandoned logging road 600 ft. up the southwest slope of Sugarloaf Mountain.

COLLECTOR: *Leonard F. Frisbie* (Tacoma 1003), May 28, 1954.

NOTE: This specimen comparable with the typical species growing in the same locality except in color of flowers.







**RECENT PUBLICATIONS OF THE  
ARNOLD ARBORETUM**

- JOHNSTON, I. M. **The Botany of San Jose Island (Gulf of Panama).** Sargentia VIII. Pp. 1-306, with seventeen plates and two text-figures. April 22, 1949. .... \$6.00
- REHDER, ALFRED. **Bibliography of Cultivated Trees and Shrubs.** Pp. i-xl. 1-825. 4°. June 14, 1949. .... \$20.00
- MERRILL, ELMER D. **Index Rafinesquianus.** Pp. i-vi, 1-296. 4°. August 8, 1949. .... \$10.00
- 

Make checks payable to the **ARNOLD ARBORETUM.**